REPRODUCTIVE PERFORMANCE OF GREAT EGRETS (*Ardea alba*) AT HIGH ISLAND, TEXAS

A Thesis

by

ANDREW JOHN MCINNES

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF MARINE RESOURCES MANAGEMENT

December 2011

Major Subject: Marine Resources Management

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Approved by:

Chair of Committee,	Susan L. Knock
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ABSTRACT

Reproductive Performance of Great Egrets (*Ardea alba*) at High Island, Texas.

(December 2011)

Andrew John McInnes, B.S., Texas A&M University at Galveston

Chair of Advisory Committee: Dr. Susan Knock

Despite habitat perturbations and seasonal fluctuations in reproduction, many studies report no significant inter-annual variation in Great Egret reproductive performance. I examined the reproductive performance of Great Egrets (*Ardea alba*) for two breeding seasons (2009 and 2010) immediately following Hurricane Ike at High Island, Texas. Breeding success, productivity, and mean brood size did not differ between years (*U*-test, $P > 0.05$). Fledging success at 21 days showed no significant difference between years, however fledging success at 28, 35, and 42 days decreased significantly between years (~15% reduction at 42 days; *U*-test, $P = 0.027$). The number of deaths per nest also differed significantly between 2009 and 2010 (0.36 and 0.95, respectively) (*U*-test, $P = 0.013$). Brood-size dependent mortality was also a significant between-year parameter (*H* test, $P = 0.003$). Successful nests in 2009 had a brood size range of 2 to 3, and of these nests, 6% and 50% experienced partial brood reduction, respectively; whereas 2010 brood size range for successful nests was 2 to 4, and 0%, 57%, and 100% of these nests, respectively, experienced partial brood reduction. Other parameters examined were water level, temperature, precipitation, prey availability, and

human disturbance. I rejected my hypothesis that habitat conditions would be less conducive to high reproductive success in 2009 than 2010, due to the impacts of Hurricane Ike. My results suggest that Great Egrets have bimodal occurrences of nestling death that are expressed as a function of brood size, hatching spread, and nestling age. Reproductive performance studies should continue through at least fledging age (42 days post-hatching for Great Egrets) to better document the reproductive performance, especially by incorporating the apparent behavioral plasticity of nestlings.

ACKNOWLEDGEMENTS

I thank my committee chair, Dr. Susan Knock, and my committee members, Dr. Bart Ballard, Dr. Wesley Highfield, Dr. Bernd Würsig, and Mr. Phil Glass, for their investment into the education of others—an appreciated legacy. Thanks also go to my friends and colleagues, plus the Marine Sciences and Marine Biology departments' faculty and staff, for making my time at Texas A&M University at Galveston an excellent experience. I also want to extend my gratitude to Winnie Burkett, and the Houston Audubon Society, for the unlimited and unfettered access to the Smith Oaks Sanctuary at High Island—the location of this study.

Finally, thanks to my wife for her patient and generous encouragement, and for her unbounded scientific curiosity and love.

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INTRODUCTION

Life history strategy of long-lived birds, such as GREGs, suggests they will adjust their reproductive effort according to prevailing environmental conditions (Herring et al. 2010). There is a large literature on various aspects of Ardeidae biology; however, their reproductive performance is not widely monitored. We lack quantitative data regarding such basic breeding information as date of nest initiation, clutch size, nest success and turnover, number of hatchlings and fledglings per nest (Pratt 1970), particularly so for GREGs.

Measurements of breeding productivity allow assessment of population stability and comparisons within and between populations (Erwin and Custer 1982), and detection of declining productivity within a population may allow timely implementation of management responses (Martin et al. 1997). However, Glass (1994) cautions that there is difficulty in accurately determining population trends of colonial waterbirds, and that change in population numbers are subject to an assortment of factors.

Breeding performance studies of GREGs have been conducted in several states, including California (Pratt 1970, 1972, 1974; Pratt and Winkler 1985; Kelly et al. 1993, 2008), Connecticut (Heath and Parkes 2002), Florida (Scott 1887; Wiese 1975; Maxwell and Kale 1977; Frederick and Collopy 1989a, b; Simon et al. 2006; Herring et al. 2010), Georgia (Teal 1965), Kansas (Gress and Schaefer 1984; Dwyer 1988; Thompson and

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This thesis follows the style of The Auk.

Ely 1989; MacCarone 1993), Louisiana (Simmons 1959; Wiese 1975), New Jersey (Gladstone 1979), North Carolina (McCrimmon 1978), Oklahoma (Sallee 1982), and Tennessee (Gersbacher 1939). However, few breeding biology data are available for Texas (examples include Goering and Cherry 1971; Taylor and Michael 1971; Chaney et al. 1978; Morrison and Shanley 1978; Mock 1984, 1985; Mock and Parker 1986). International GREG breeding studies include Australia (Baxter 1994; Maddock and Baxter 1991), Brazil (de Toledo 2000), Mexico (Gladstone 1979), and Rhodesia (Tomlinson 1976).

The Great Egret—an Ardeidae (*Ardea alba*) in the order Ciconiiformes along with ibises, spoonbills, storks, and others—is a common wading bird along the coast of the USA. It is a large white bird with long legs, neck, and bill, short, rounded tail, and long, broad wings (Elphick et al. 2001). Total length ranges 94-104 cm, body mass is approximately 1 kg, and wingspread is around 140 cm (McCrimmon et al. 2001).

Great Egrets are high trophic level predators (Kushlan 1979, 1993), largely aquatic in their foraging habitats, and utilize habitats such as marshes, swamps, streams, rivers, ponds, lakes, impoundments, lagoons, tidal flats, canals, ditches, and fish-hatchery ponds (McCrimmon et al. 2001; Houston Advanced Research Center 2010). These opportunistic foragers are generalist exploiters (Elphick et al. 2001; McCrimmon et al. 2001; Gawlik 2002; Herring 2008; Herring et al. 2010) though specialty piscivores (Mock 1984, 1985; Elphick et al. 2001), but also consume invertebrates—particularly crustaceans—along with amphibians, reptiles, birds, and small mammals (Elphick et al.

2001; McCrimmon et al. 2001). Kushlan (1976) summarized foraging behaviors of egrets, including adaptability to differing habitats and prey availability.

Food availability is a primary limitation to avian populations, particularly during breeding seasons (Lack 1947; Skutch1949; Brown 1964; Newton 1980; Nagy and Holmes 2005), presumably because of elevated adult physiological requirements for egg production and food supply to nestlings (Herring 2008). Most avian species' breeding coincides with seasons of maximum food availability (Lack 1947; Herring 2008).

GREGs are primarily colonial nesters, usually proximal to wetland foraging sites (Baicich and Harrison 1997; Elphick et al. 2001). Islands, including dredge-spoil islands, are favored colony sites, presumably because they offer enhanced protection against mammalian predators (Elphick et al. 2001)—as little as 5-10 cm of water substantially restricts the travels of most terrestrial predators (Frederick and Collopy 1989b). Colony sites that lack a substantial water barrier are few (Chapman and Howard 1984).

Seasonally monogamous pair bonds are formed through elaborate courtship displays at the nest site, including displays of nuptial plumage (aigrettes) (Mock 1984; Elphick et al. 2001). For a thorough description of GREG reproductive behaviors, see Wiese (1975, 1976) and also McCrimmon (1974) and Mock (1980). In North America, a single brood is produced per year under ordinary circumstances (Baicich and Harrison 1997; Elphick et al. 2001; McCrimmon et al. 2001). However, the complete loss of nest or nestlings may result in initiation of a second nest (A. J. McInnes field notes, but see also Pratt 1972; Maxwell and Kale 1977; Mock and Parker 1986).

Clutch size varies from one to six (usually 3-4) (Pratt and Winkler 1985; Kaufman 1996; McCrimmon et al. 2001) though Baicich and Harrison (1997) state 4-5, sometimes 3-6 eggs, and Frederick (2002) reports a clutch size of 2-4 eggs. GREGs asynchronously lay pale-blue/greenish-blue eggs (Weise 1975; Kaufman 1996; Baicich and Harrison 1997) with the last egg generally smaller than others in the clutch (Custer and Frederick 1990). Eggs are laid at 1 to 2 day intervals (Jenni 1969; Mock 1985; Dwyer 1988)—Maxwell and Kale (1977) reported an average of 1.9 days at Riomar Island, Florida, and Weise (1975) reported 2 day intervals at Avery Island, Louisiana.

Incubation typically begins after the first or second egg has been laid (Wiese 1975; Mock 1984, 1985; Custer et al. 1992; Kaufman 1996; Elphick et al. 2001), and the nidoculous (young that remain in the nest after hatching) chicks hatch asynchronously. Kaufman (1996) and Baicich and Harrison (1997) report 23-26 days of incubation, though Morrison and Shanley (1978) listed 23-27 days for a GREG rookery at the nearby Sabine Lake, TX. Maxwell and Kale (1977) reported an incubation period of 26 days. However, Frederick (2002) reports an incubation period of 26-27 days, and Custer et al. (1992) report a mean incubation period of 27.3 days (n = 18 eggs), which is very similar to the 27.2 days reported by Weise (1975).

Hatching intervals vary depending on laying spread, onset of incubation, and clutch size. McCrimmon et al. (2001) report a hatching range of 1-7 days. Chick hatching order is reported here as A-chick (first hatched), B-chick (second hatched), and so on. Weise (1975) reported 15.7 hours and < 26 hours between A- and B-chicks for two different subsets of clutches, and 48.2 and < 55 hours between B- and C-chicks and

C- and D-chicks, respectively. Maxwell and Kale (1977) reported an average hatching interval of 0.9 days for A- and B-chicks, 2.0 days for B- and C-chicks, and 3.0 days for C- and D-chicks. Mock (1985) reported hatching intervals between A- and B-chick, B- and C-chick, and C- and D-chick of 1.3, 1.7, and 2.1 days, respectively. Nestlings are brooded constantly—parents alternate—until the youngest is about three weeks old (Wiese 1975; Mock and Parker 1986). At that age, nestlings are apparently homeothermic and able to evade predatory threats. Fledging (a young bird is said to have fledged if it is capable of flight, departs the nest for short periods, yet returns to the nest for food and roosting) occurs 42-49 days post-hatching (Kaufman 1996; Baicich and Harrison 1997) and the total nestling period extends to 62-70 days (Wiese 1975) or 75-85 days (Frederick 2002).

It is reported that prey availability is the most likely proximate variable to control both the size and distribution of populations (McCrimmon et al. 2001). As such, quality foraging habitat proximal to breeding colonies is an important aspect driving the general health of colonial wading birds (Custer and Galli 2002); nesting wading birds are constrained to forage relatively close to the colony; therefore, for a colony to be successful, it must be located near areas that provide sufficient food for the approximately 3 month breeding cycle (Bancroft et al. 1994; Custer and Galli 2002).

Water conditions and prey abundance influence foraging site selection by breeding wading birds (Bancroft et al. 1994). There are several reports of GREG flight distances from colony site to foraging areas, yet the range of reported distances has considerable variability in distance (Bancroft et al. 1994). Median foraging flight

distance from colonies in the United States range from 3.7 km in the Florida Everglades (Smith 1995), to 13.5 km in North Carolina (Custer and Osborn 1978) and east central Minnesota (Custer and Galli 2002). Maximum foraging flight distances exceed 40 km (Bancroft et al. 1994) (Table 1).

Several of these foraging distance studies are in areas where hydrologic fluctuations are highly variable, such as the Florida Everglades (Bancroft et al. 1994; Beerens 2008; Herring et al. 2010) and coastal North Carolina (McCrimmon 1978). However, little was known about how these factors influence GREG nesting success (Bancroft et al. 1994) until the work of Herring (2008) and Herring et al. (2010). For those locations where water levels are highly variable it is typically reported that GREGs fly farther to forage during high tide than at low tide (Custer and Osborne 1978; Bancroft et al. 1994; Wong et al. 1999; Beerens 2008; Herring et al. 2008).

Unlike the Florida Everglades, the upper Texas coast experiences little fluctuation in water levels, though flooding does occur. Salt marshes in this region are often flooded during the spring as a result of some combination of wind-forcing, freshwater inflows, and the very gradual bathymetric and topographic relief. Spring flooding coincides with times of extensive marsh use by transient nekton, often for

completion of critical life stages and further development (Minello and Rozas 2002). Prey abundance and distribution in this region are unlikely to be as unpredictable as in areas dominated by highly variable hydrological regimes.

The upper Texas coast is characterized by fair weather astronomical tides ranging from 0.3 to 0.6 meters and relatively low amplitude waves with periods ranging between 4 to 6 seconds (Morton and McGowen, 1980). Wave energy is generally low to moderate, with most significant wave heights being < 0.6 m; shallow waves > 1 m occur less than 1% of the time and storm waves are typically < 1.8 m high (United States Army Corps of Engineers, 1983). The microtidal nature of the upper Texas coast is dominated by a diurnal/mixed tidal signal with diurnal range (Mean Higher High Water (MHHW) - Mean Lower Low Water (MLLW)) of 0.43 m and mean range (Mean High Water (MHW) – Mean Low Water (MLW)) of 0.31 m as measured at Galveston Pleasure Pier (National Oceanic and Atmospheric Administration 2003). Thus, coastal wetlands along the upper Texas coast provide stable foraging habitats for wading birds such as GREGs.

Table 1. Reported flight distances between breeding colony and foraging sites by Great Egrets.

Median (km)	**Maximum (km)**	**Mean (km)**	**Colony location**	**Source**	**Comments**
5.15 [a]	> 40	6.3	Florida Everglades (12 colonies)	Bancroft et al. 1994	-
13.5	27.8	3.6 [a]	Nth Carolina	Custer and Osborn 1978	"most" < 4.0 km
13.5	30.3	-	East central Minnesota	Custer and Galli 2002	minimum = 4.0 km
3.7	33.3	-	Lake Okeechobee, Florida	Smith 1995	-
4.0 [b]	-	-	Galveston Bay, Texas	Glass 1994	-
-	-	8.1	Florida Everglades	Beerens 2008, Herring et al. 2010	consecutive years
		4.6			
-	-	7.98	Florida Everglades	Herring 2008	consecutive years
		4.83			
5.6	10.7	6.2	Indian River Lagoon, Florida	Stolen et al. 2007	-
1.24 [c]	8.0	-	China	Wong et al. 1999	-

[a]Calculated from data in the original publication. [b]Is reported as "foraging area" radius around colonies. [c] Highest reported value for two year study.

Mock (1984, 1985) reported that GREG nestlings at a Texas rookery were fed a bolus that typically contained 5-15 fish with median length of 50 mm and mass of 2 g each (mean = 4.4 g) which are stuck together by mucus. In their study in Galveston's West Bay, Minello and Rozas (2002) reported a mean total fish length of 26.6 mm with 97% of the specimens < 100 mm (range 4-330 mm), which aligns well with the bolus measurements of Mock (1984, 1985).

For the first week post-hatching, young are fed throughout the day. After that period, they are fed predominantly following nest relief (see also Wiese 1975). Mock

(1985) reported that from an observed 1,036 feedings, GREGs provided an average of 2.58 boluses per feeding at three rookery islands in Port Lavaca, Texas. Wiese (1975) reported 5.7 average (maximum = 9) daily feedings up to age 35 days, thereafter reduced to 2-3 per day.

GREG siblings rapidly form dominance hierarchies that are stable and age-dependent, conferring a considerable feeding advantage to the older (and larger) siblings (Mock 1984). Brood size is reported here as BS/4 (brood size of 4), BS/3 (brood size of 3), and so on. Mock and Parker (1986) reported, for BS/3, that survival rates to 25 days of A-, B-, and C-chicks were 88%, 82%, and 62%, respectively. However, if either elder sibling died, then the C-chick's survival jumped to 86%. A younger sibling's death only marginally increased the respective survival of A- or B-chicks.

During the first two weeks post-hatching, parents deposit the food bolus onto the nest floor (Wiese 1975; Mock 1984), whereby the nestlings peck off small chunks in shared feeding. Upon cessation of feeding, the parent will re-consume the remaining bolus, presumably for later feedings. However, a switch from "indirect" to "direct" feeding begins at age 7 days (Wiese 1975; Mock 1984), which becomes the predominant method by age 24 days (Mock 1984). As a result of small prey size, these directly-fed boluses are passed directly into the gullet, thereby enabling senior chicks to monopolize the food (Wiese 1975; Mock 1984, 1985; Mock and Parker 1986). Consequently, during the first three weeks, individual junior siblings have a significantly higher risk of not getting any food; A- and B-chicks each receive greater than a third of the food available and the C-chick receives "much less" than one third of the food (Mock 1985). At Port

Lavaca, Texas, differential growth rates were recorded in BS/3, whereby 25-day-old C-chicks weighed on average 30% less than its A- and B- siblings at the same age (Mock 1985).

For GREGs, active brood reduction by siblings (siblicide – Mock 1984) generally occurs in the nest and is based on size hierarchies when brood sizes are greater than 2 young (Mock and Parker 1986, 1997). Avian brood reduction can occur as either obligate or facultative (Edwards and Collopy 1983); the deaths result from the combined effects of physical beating and socially enforced starvation by (usually) older siblings (Mock 1984). Siblicide appears to be the cause of most deaths in GREG brood reductions (Mock 1984) and "about" one third of C-chicks die, either directly or indirectly, from the beatings from older siblings (Mock 1982). However, Mock and Parker (1986) found that GREG fighting rates in BS/2 nests were significantly lower than in B/3 or B/4 nests, and Godfray (1986) reported the level of aggression in GREG nestlings declined "markedly" after the number of nestlings was reduced to two.

In an extensive literature review, O'Connor (1978) found that brood-size dependent mortality had extensive empirical support. When clutch sizes increase, egret nestlings become more violent and first-hatched nestlings (A-chick) often kill siblings (Mock 1982, 1984; Mock and Parker 1986, 1997; Herring et al. 2010), and highest mortality occurs amongst the youngest nestlings (O'Connor 1978; Mock 1982, 1984, 1985; Mock and Parker 1986).

The objectives of this study were twofold: 1) quantify the reproductive performance parameters of GREGs at this rookery in order to test the hypothesis that

Hurricane Ike negatively impacted the breeding performance of GREGs at this rookery in 2009, and 2) determine whether brood size and hatchling death rates were related (i.e., brood-size dependent mortality). This study site was selected for its proximity to my academic institution, ease of observation, lack of human disturbance to the breeding birds, and the ability to use a non-invasive method of data collection, thereby allowing me to address the objectives of the study.

Study Area

High Island—not actually an island—is named for the salt dome that uplifted the immediate area above the rest of the Gulf Coast. At 11.6 m elevation, it is the highest location on the coast between Mobile, Alabama, and the Yucatán Peninsula. The Town of High Island is located on the eastern extreme of Bolivar Peninsula at the very eastern extent of Galveston County, on the Upper Texas Coast (Daniels 2010) (Fig. 1). The surrounding area is an extensive landscape of salt-marshes, aquatic wetlands, and somewhat ephemeral agricultural ponds.

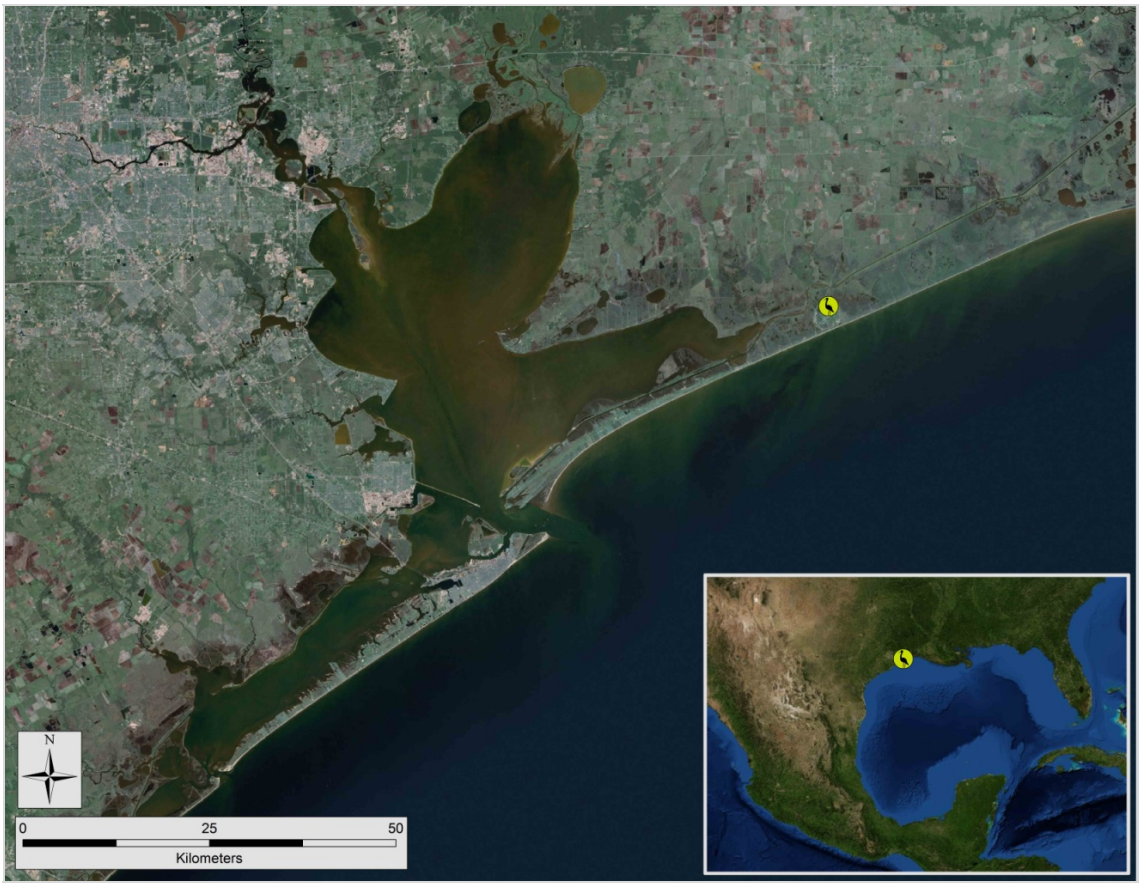

Fig. 1. Aerial image of the upper Texas coast, showing location of High Island, Texas (yellow circle). Inset image shows High Island (yellow circle) and the Gulf of Mexico. Topographic and aerial images from Environmental Systems Research Institute (ESRI 2011).

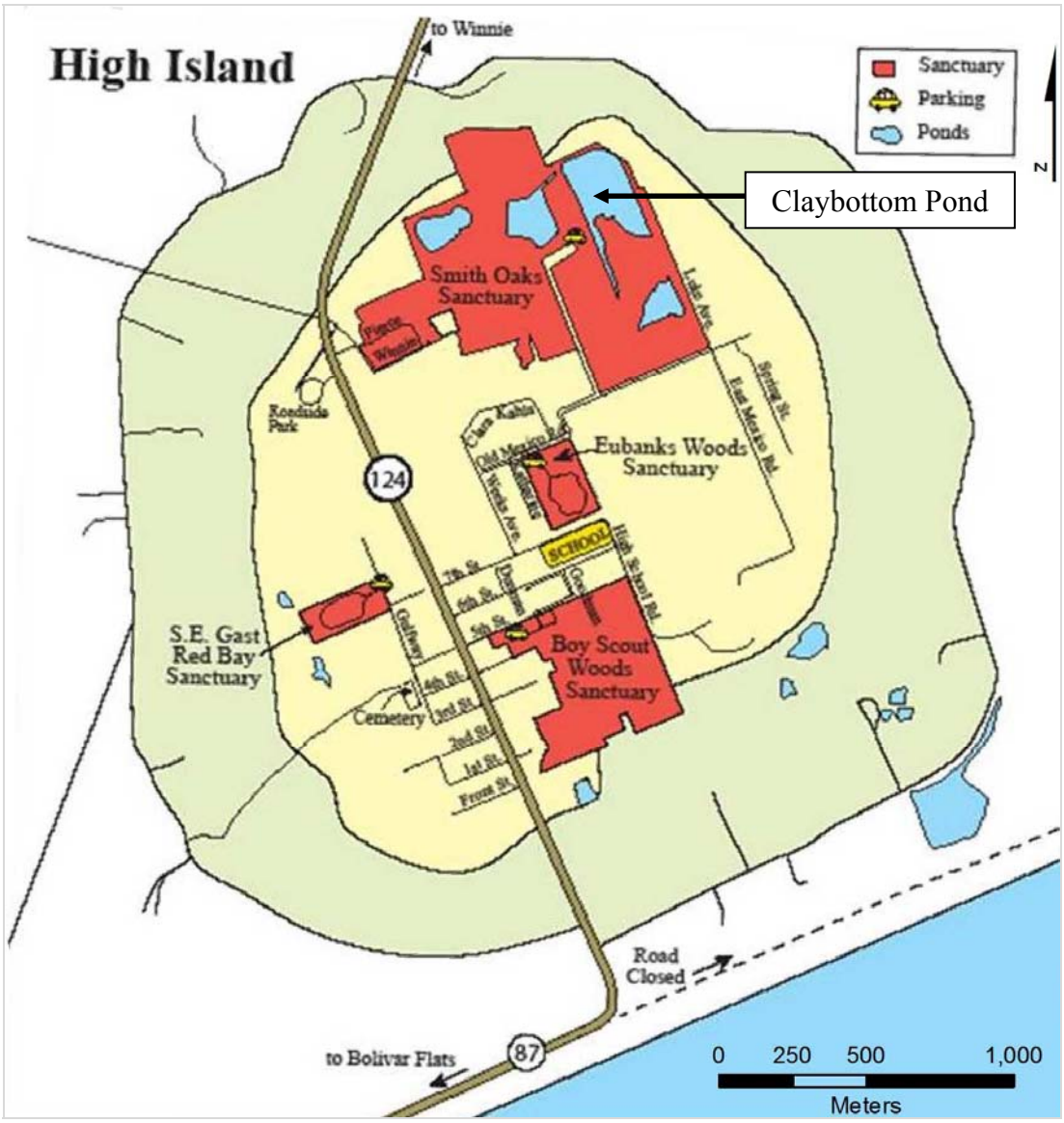

Fig. 2. Schematic of Houston Audubon Society's High Island Sanctuaries (Houston Audubon Society 2011).

In 1994, the Amoco Corporation donated land, including Claybottom Pond/Heron Island, to the Houston Audubon Society (HAS) who now manage the land as four sanctuaries (W. Burkett pers. comm.) (Fig. 2). These sanctuaries are nationally and internationally known destinations for birdwatchers, particularly during spring migration and colonial waterbird breeding season (Daniels 2010).

One of these sanctuaries, the 177.33 acre Smith Oaks, contains a man-made freshwater pond—Claybottom Pond—which has within it an island named Heron Island (29.575 °N, -94.390 °W) (Figs. 3A, 3B). Heron Island consists of a U-shaped clay structure which rises approximately 2.5 meters above the mean freshwater level of Claybottom Pond (W. Burkett pers. comm.). Approximate 2-dimensional surface area of the island is 3,000 m^2. Claybottom Pond, like all the ponds in Smith Oaks, is man-made, originally constructed for supplying the town of High Island with water and to supply a former sulfur plant. These ponds have become an important refuge for wildlife as there is little other permanent fresh water in the area (W. Burkett pers. comm.).

Fig. 3A. Aerial photo of Claybottom Pond showing Heron Island (circa 2004). Color infrared aerial imagery sourced from Texas Natural Resource Information System (TNRIS 2010).

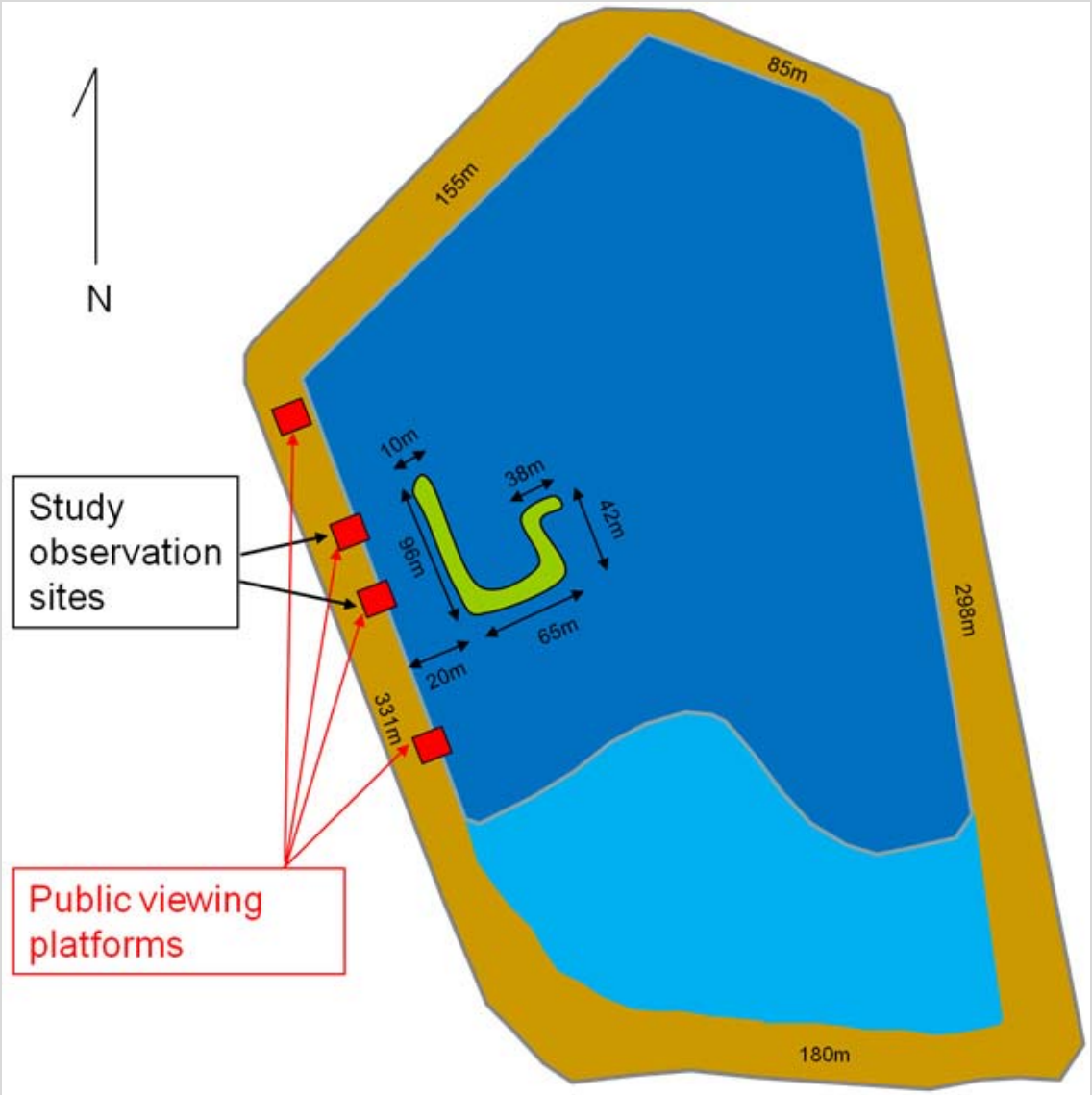

Fig. 3B. Schematic of Heron Island in Claybottom Pond, Smith Oaks Sanctuary including observation platforms (red squares). The dark blue polygon approximates the water level during the two-year period of this study. The light blue polygon approximates extent of water during high water levels, the green polygon is Heron Island, and the olive/tan polygon illustrates the containing banks of pond.

When the land was deeded to HAS, there were no birds nesting on Heron Island. HAS maintains a "no hunting" policy and in 1995, one year after HAS assumed management of the sanctuaries, there were 50 heron nests on the island and birds commenced roosting on the island at night. The island lacks terrestrial predators and wading birds have continued to nest on Heron Island every year since 1995 (Texas Colonial Waterbird Survey unpubl. data).

The first Great Egrets nested on Heron Island in 1997 (n = 10 nests), a portion of the approximately 330 pairs of colonial waterbird species nesting on the island that year (Texas Colonial Waterbird Society unpubl. data). By 2004 Heron Island was a mixed-species rookery with approximately 1,200 pairs of birds, comprising 10 species, nesting on the island—Great Egrets comprised 381 nests (Texas Colonial Waterbird Society unpubl. data).

This island has experienced substantial and ongoing loss of flora since the mid 1990's—a result of numerous tropical cyclones and bird-guano induced soil acidification and leaf-burn ("guanotrophication" – (Telfair and Bister 2004)). Hurricanes strike the Texas coast with moderate frequency, averaging 0.67 hurricanes per year since 1900 (Hayes 1967; in Davis 1972, and Morton and Paine 1985). Historical records clearly show that this area of the Texas coast will receive minor storm damage every few years and extreme storm damage about every 20 years (Morton and Paine 1985).

The historic vegetation at this rookery were pecan (*Carya illinoinensis*), hackberry (*Celtis laevigata*), willow (*Salix* spp.), and yaupon (*Ilex* spp.), since replaced primarily by the invasive Chinese tallow (*Triadica sebifera*) and the rattle bean

(*Sesbania* spp.) (W. Burkett pers. comm.). Recently, winds from Hurricanes Rita (2005) and Humberto (2007), in combination with continued guanotrophication resulted in an acceleration in the reduction in tree and shrub density on the island (W. Burkett pers. comm.) (Figs. 4A-4C).

Fig. 4A. Heron Island, June 1997. Great Egrets and other egret species are nesting among tall and dense stands of mature trees (image courtesy of Winnie Burkett).

Fig. 4B. Heron Island, June 1999. Great Egrets and other egret species are nesting among tall and dense stands of mature trees (image courtesy of Winnie Burkett).

Fig 4C. Heron Island, March 2010, showing loss of trees from cumulative effects of multiple hurricanes and guanotrophication.

Additionally, this site and surrounding areas were heavily impacted by climatic events through 2008-2009; winds from Hurricane Ike caused a drastic reduction of the remaining trees within the rookery in September 2008 (Fig. 4C), and neighboring areas were inundated by saltwater as a result of the storm surge (Figs. 5A, 5B). These perturbations have thus impacted nest site availability at this site specifically and throughout the upper Texas coast in general—a region that is nest site limited compared to historic options (P. Glass pers. comm.).

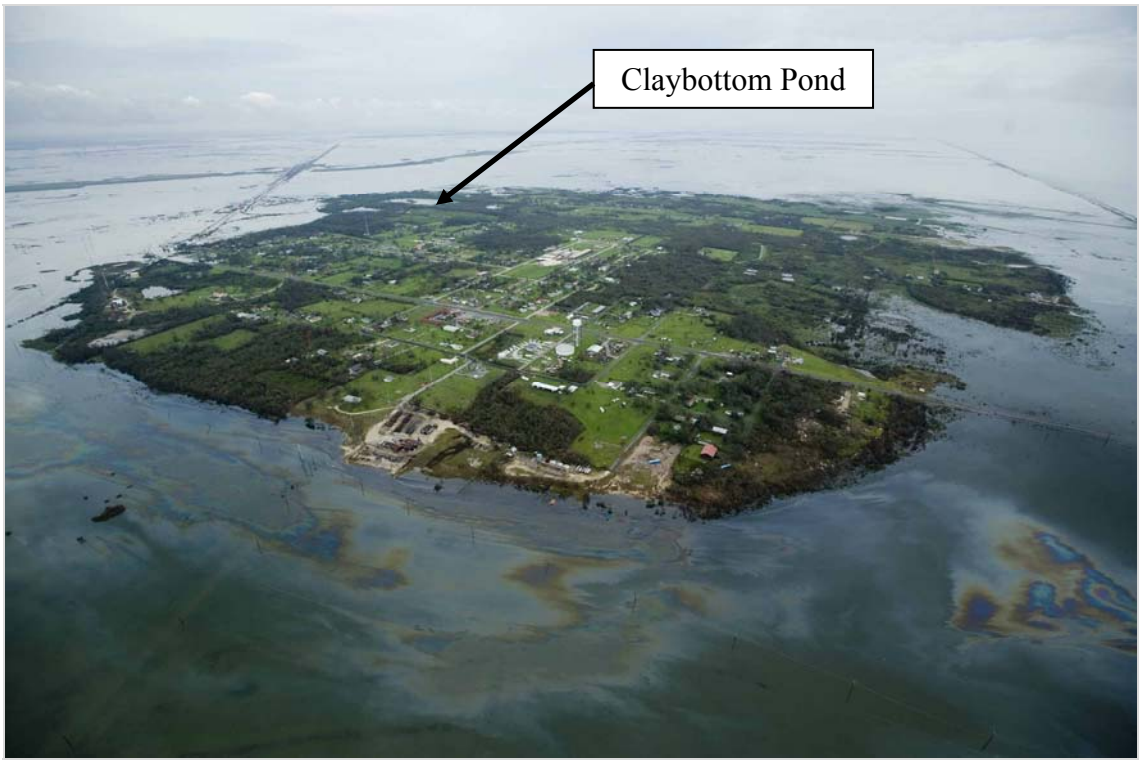

Fig. 5A. Aerial photo of High Island, Texas taken 09/14/2008 - the day after Hurricane Ike made landfall. The image shows retreating flood water and regional inundation by saline Gulf of Mexico waters, and local oil seeps. Black arrow indicates Claybottom Pond. The beachfront and Gulf of Mexico can be seen in the upper right corner. Image by Smiley N. Pool (Houston Chronicle 2008) – used with permission.

Fig. 5B. False-color infrared aerial images of High Island region before (August 15, 2006 on left) and after (September 28, 2008 on right) Hurricane Ike. Living vegetation is displayed in red (the brighter the red, the more robust the vegetation); innundated (i.e. denuded) areas are in blue-green tones. High Island is indicated by yellow circle. The gray, black, and red rings indicate different radii from Heron Island rookery: 10, 15, and 20 km, respectively. Image courtesy National Aeronautics and Space Administration (NASA 2008).

Wading bird productivity often fluctuates between years. Following hurricanes, breeding colonies of wading birds have a higher probability to become inactive or experience large population shifts when compared to the pre-hurricane period (Shepherd et al. 1991; Leberg et al. 2007). As such, quantification of reproductive performance parameters likely allows assessment of a population's stability and perhaps comparisons among and within populations (Erwin and Custer 1982). As a consequence of the saltwater inundation and other perturbations associated with Hurricane Ike in September 2008, I hypothesized that the 2009 reproductive performance of GREGs at Smith Oaks rookery would be depressed. As there were no existing data for this rookery, a two-year study was devised to compare and contrast these reproductive performance parameters with values in the published literature.

METHODS

Data Acquisition

GREG nests were monitored during 2009 (n = 25) and 2010 (n = 22) at Heron Island, in Houston Audubon Society's (HAS) Smith Oaks Sanctuary at High Island, Texas. Field observations occurred February 2nd - June 27th, 2009 and February 22nd, 2010 - July 9th, 2010. Observations were conducted every two-weeks during February and March; upon commencement of breeding behavior, data were gathered tri-weekly during daylight hours until completion of the nesting season. Ages reported refer to the number of days since the first hatchling was observed, on a per nest basis. That is, the first nestling in each nest is the "A-chick", the second is "B-chick", and so on. However, as observations were not conducted daily, all events occurring in-between visits were recorded as occurring on the day of visit to the rookery. The rookery was observed on 38 days in 2009 and 37 days in 2010 for approximately 75 hours each season.

After nest establishment (post pair-bond formation) and onset of incubation, GREG nests were identified and numbered on a composition panoramic digital image of the rookery, thereby enabling repeated observations of defined nests (Fig. 6). Over the course of each season, the foliage would obscure some of the initially observed nests; monitoring of these nests was subsequently discontinued. Later nesters (and/or re-nesters) were added to the study as nest visibility allowed, and observations follow the procedure stated above.

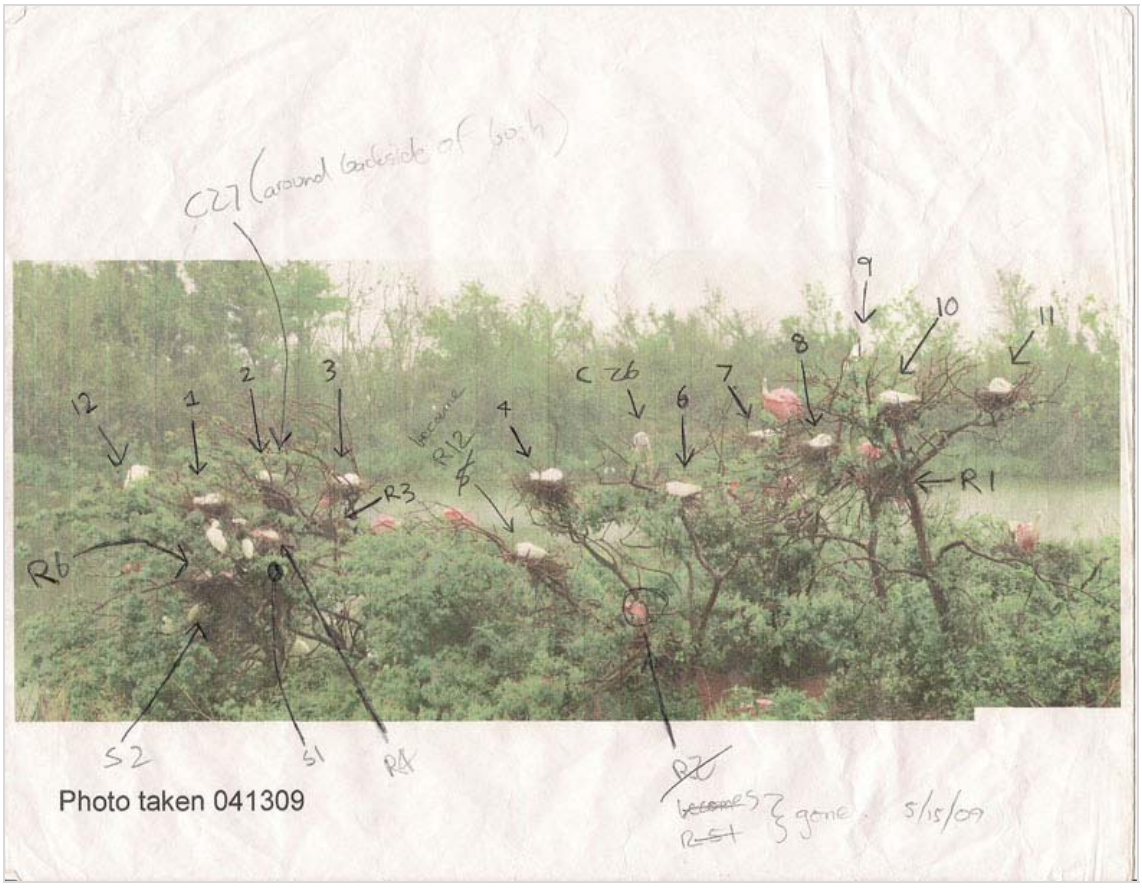

Fig. 6. Sample field sheet illustrating nest identification and numbering at Heron Island.

Fledging Success

Though studies of GREG reproductive performance exist, definitions of fledging vary among authors (see summary in McCrimmon et al. 2001). Consequently, these various studies incorporate differing durations of study, typically < 42 days. This is because hatchlings are often difficult to monitor as they mature because older chicks, from approximately 2-3 weeks of age—colloquially termed "branchers"—are inclined to clamber away outside the immediate nest (Teal 1965; Burger 1982; Elphick et al. 2001),

and fledglings are taking short flights around the rookery area (Wiese 1975; Frederick 2002). Consequently, determining whether a particular nest successfully fledged any young is difficult (Martin et al. 1997). As such, investigators typically use calculations based on the young reaching some prescribed number of days, typically less than fledging age (Burger 1982; Erwin and Custer 1982). These differing criteria create a problem when comparing fledging success between different studies.

Examples of nestling ages when young considered fledged or nest considered successful include 10 days (Maxwell and Kale 1977), 15 days (Herring 2008; Herring et al. 2010), 17 and 31 days (Gladstone 1979 – two separate study sites), 21 days (Frederick and Collopy 1989a), 25 days (Mock 1985; Mock and Parker 1986), 35 days (Heath and Parkes 2002), 42 days (Dwyer 1988), 28-49 days "prefledging" (Kelly et al. 1993), 49 days (Pratt and Winkler 1985), 42-56 days (Baxter 1994), and 52 days (Wiese 1975). Other studies report that GREG observations continued until fledging, but provide no metric or definition (e.g., Teal 1965; Pratt 1970, 1972, 1974; Chaney et al. 1978; Morrison and Shanley 1978; Gress and Schaefer 1984; de Toledo 2000; Parkes 2005).

My study monitored nests through at least 42 days except for three late-starting nests in 2009. The parameters I recorded were: brood size (the numbers of hatchlings), and fledglings (number of hatchlings remaining at 42 days), plus anecdotal observations (not extensive or consistently gathered, and primarily behavioral in nature). Data were recorded as happening on the day of observation, not the mid-point between observation dates. Selection of study nests for both years was *ad libitum*; nests were not randomly

chosen for this study as the topography, orientation, and size of the colony did not allow for a meaningful randomization process. Instead, only those nests with completely visible broods were included for study, and therefore may include bias related to nest concealment and location.

All data acquisition and images were recorded from the same two fixed viewing platforms situated approximately 20m from the rookery island (Fig. 3B) utilizing an 8 x 42 binocular and a 20-60x spotting scope. In both years, an 8.2 megapixel Canon digital SLR camera fitted with a 100-400mm image-stabilized lens was used to record the composition panoramic imagery, enabling subsequent nest numbering on printed images; other images provide a temporal and spatial reference of the rookery dynamics throughout the study periods.

Yearly nest counts (Texas Colonial Waterbird Society unpubl. data) were provided by Winnie Burkett, Sanctuary Manager HAS - retired, who, along with assistants, conducted the annual Texas Colonial Waterbird Survey for this site (Colony # 600-270) following a protocol established by the United States Fish and Wildlife Service (USFWS) (see Glass and Roach 1997; Blacklock and Slack 1979). This annual survey of the Texas coast's colonial waterbirds is regarded as one of the most complete and long-term data sets available, with nesting populations for the years 1973-present (United States Geologic Survey (USGS) National Biological Information Infrastructure 2011).

Prey Availability

Estuarine prey abundance was obtained from Texas Parks and Wildlife Department (TPWD) Coastal Fisheries Division – Dickinson, TX. Since 1976, the TPWD has conducted regular and extensive sampling of finfish and other organisms that inhabit Texas bays and estuaries using a randomized sampling method (American Fisheries Society 2005; Houston Area Research Center 2010). This "fishery-independent" sampling is designed to provide statistically precise estimates of target species (American Fisheries Society 2005).

To determine the abundance of estuarine prey resources in this colony's foraging area, the fish per hectare of this prey species guild was calculated from TPWD bag seine data for minor bay #150 (TPWD unpubl. data). Fisheries data were collected with four different sampling gear types of which the bag seine provides data most appropriate for this study (W. Balboa, Texas Parks and Wildlife Department pers. comm.) because this equipment best captures juvenile and small adult species in shallow, shoreline habitats (Houston Area Research Center 2010). These marsh-edge habitats—a prime foraging areas of GREGs— have shown a pattern of high nekton densities along Gulf Coast marshes (Rozas 1993; Minello and Rozas 2002). The bag seines the TPWD uses are 18.3 m long, 1.8 m deep, and the bag is constructed of 13 mm mesh. The seine net is deployed and pulled parallel to shore for a distance of 15.2 m (Houston Area Research Center 2010).

TPWD sampling sites were mapped in ArcGIS 9.3 whereby prey density/abundance were calculated using only those sampling sites that were within 20

km of the High Island colony (Fig. 7). This 20-km buffer is only partially arbitrary: it equates to 50% of the maximum foraging flight distance for breeding GREGs reported in the literature (Table 1), thereby allowing conservative estimates of estuarine prey availability. For this analysis, only prey abundances encompassing May-July were examined, as these months cover the great majority of the GREG hatchling period. These data were subsequently filtered to 11 low-trophic level fish species (selected as a proxy for the primarily piscivorous diet of GREGs) that historically dominate abundances in marsh/near-marsh habitats of Galveston Bay. These filtered data were then pooled by month and subsequently standardized by seine width, tow length and duration of tow, thereby allowing analysis in the form of fish abundance per hectare in marsh/near-marsh habitats of Galveston Bay.

The fish species comprising this prey guild were: bay anchovy (*Anchoa mitchilli*), Atlantic croaker (*Micropogonias undulatus*), striped mullet (*Mugil cephalus*), sheepshead minnow (*Cyprinodon variegatus*), Gulf menhaden (*Brevoortia patronus*), spot (*Leiostomus xanthurus*), inland silverside (*Menidia beryllina*), pinfish (*Lagodon rhomboides*), Gulf killifish (*Fundulus grandis*), longnose killifish (*Fundulus similis*), and silver perch (*Bairdiella chrysoura*). Prey availability in palustrine and riparian (freshwater) habitat was not included in this study.

Abiotic data— monthly values for temperature (highs and lows) and precipitation—were graphically analyzed to determine if the values differed significantly between-years and also against the 30-year average. The standard deviation was

calculated for the 2009 and 2010 data and visually compared by error-bar overlap with the 2010 and 30-year values.

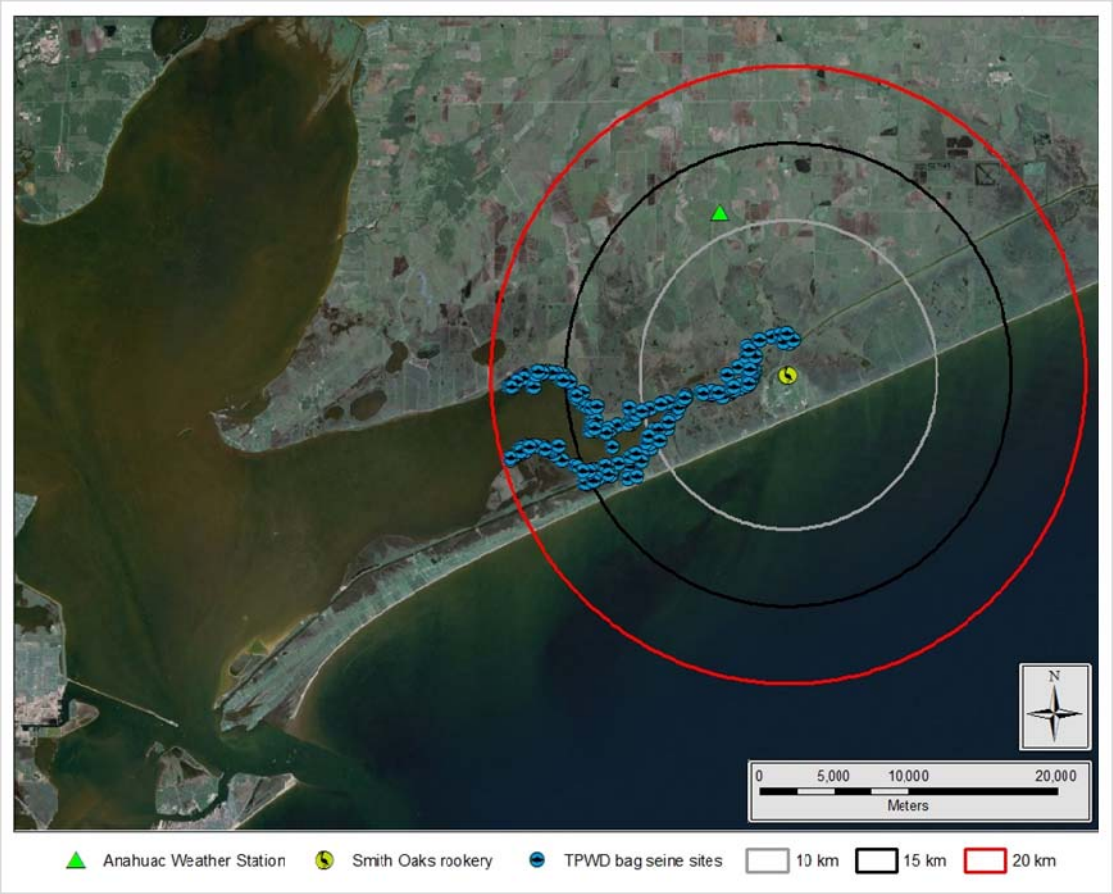

Figure 7. Aerial image of Galveston Bay, illustrating locations of TPWD estuarine bag seine sites (blue dots) used in quantifying fish abundance for 11 selected species. The Great Egret rookery at High Island is indicated by the yellow dot. The Anahuac Weather Station is indicated by the green triangle. Background image courtesy Environmental Systems Research Institute (ESRI 2011).

Statistical Analyses

All statistical analyses were conducted using SPSS for Windows (Version 16.0, 2007). Due to the ordinal nature of reproductive performance (count) variables, their non-normal distribution, and small sample size, the assumption of normality would be violated. As such, non-parametric tests were conducted for these analyses. The significance level for all tests was $\alpha = 0.05$.

The Mann-Whitney U-test (*z* statistic) was conducted on breeding success, brood size, adjusted brood size, fledging success, adjusted fledging success, productivity, adjusted productivity, and deaths per nest. This test examines if there is a statistically significant difference between the underlying distributions (medians) of two data sets. For the null hypothesis that a parameter has the same median for both years, a large *P* value (> 0.05) suggests the data do not give any reason to conclude that the overall distributions (medians) differ.

The Kruskal-Wallis test (*H* statistic) was used to test deaths per brood size. This test examines differences in location in ranked data that are grouped by a single classification (Sokal and Rohlf 1995). If the null hypothesis that all groups (e.g., for test of deaths by brood size, brood size contains the groups) do not differ in rank-order (i.e., similar rank sums) has a resultant *H* statistic that differs greatly from the calculated χ^2 value (i.e., small *P* value) then I can confidently reject the null hypothesis and conclude that the groups differed between the two years sampled (Sokal and Rohlf 1995).

For the tests of fledging success (FS/21, FS/28, FS/35, and FS/42 days), data are entered as a ratio fraction: for a given nest that had a brood size of 3 and still had 3

nestlings at 21 days, that nest would be recorded as having a fledging success (21 days) of 1 (i.e., 3/3). If, however, there were only 2 remaining nestlings at 21 days then the FS/21 value would be recorded as 0.667 (i.e., 2/3). This procedure was repeated for all nests at all "fledging" ages. Fledging success was calculated by dividing the number of fledglings by brood size for each brood size category. This method allowed for comparison with reported and/or calculated values from the literature.

RESULTS

Breeding Chronology and Reproductive Performance

For the 2009 breeding season, 8 species of colonial waterbirds occupied 360 nests within the rookery, of which GREGs totaled 77 nests. These nesting species were: Great Egret (*Ardea alba),* Neotropic Cormorant (*Phalacrocorax brasilianus*), Anhinga (*Anhinga anhinga*), Snowy Egret (*Egretta thula*), Little Blue Heron (*Egretta caerulea*), Tricolored Heron (*Egretta tricolor*), Cattle Egret (*Bubulcus ibis*), and Roseate Spoonbill (*Platala ajaja*) (Table 2). During the 2010 spring breeding season, the same 8 species occupied 683 nests within the rookery, of which GREGs totaled 110 nests (Texas Colonial Waterbird Society unpubl. data).

The mean GREG breeding population for this rookery since its first utilization as a rookery by GREGs in 1997 was 130 nests (range 10 - 381) (Fig. 8). Over this same time period the mean breeding size of all colonial waterbird species was 659 nests (range 305 - 1194) at this rookery (Texas Colonial Waterbird Society unpubl. data) (Fig. 9). The first GREG nestling in the sample nests for each season was observed on April 19, 2009 and April 18, 2010.

Table 2. Counts of Great Egret and other colonial waterbird species nests on Heron Island at Smith Oaks Sanctuary for 2009 and 2010 breeding seasons (Texas Colonial Waterbird Society unpubl. data).

SPECIES	**2009**	**2010**
Great Egret	77	110
Neotropic Cormorant	141	246
Anhinga	1	1
Snowy Egret	29	44
Little Blue Heron	6	1
Tricolored Heron	34	22
Cattle Egret	15	169
Roseate Spoonbill	57	90
TOTAL	**360**	**683**

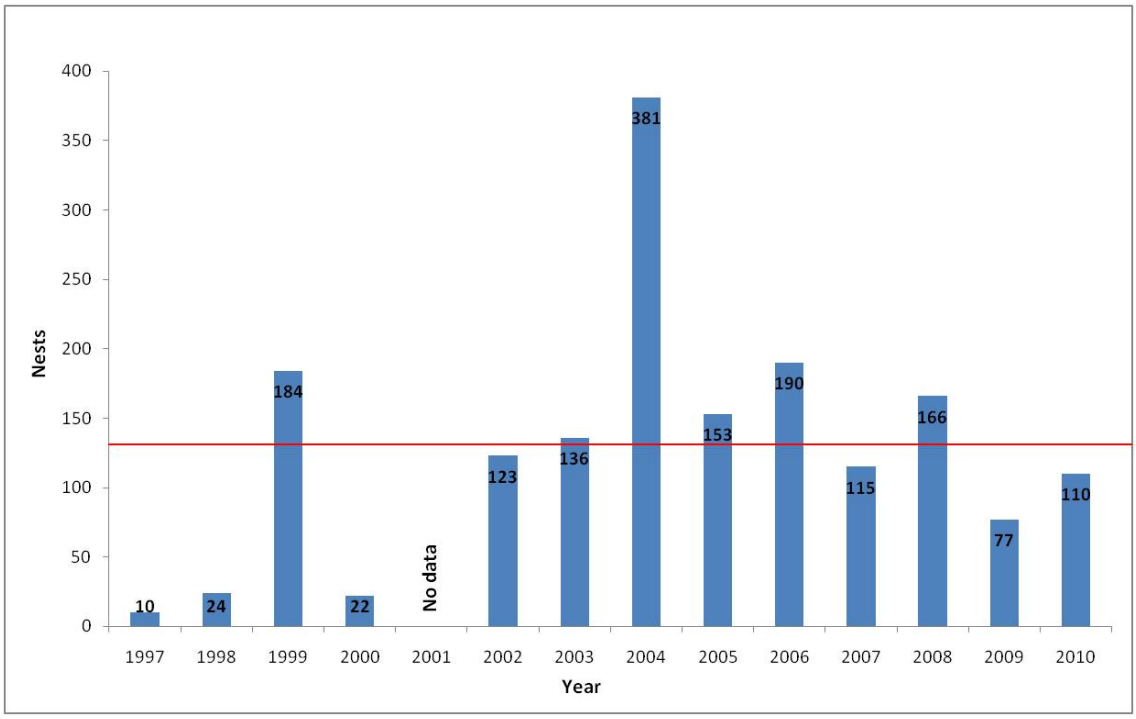

Fig. 8. Number of Great Egret nests at Heron Island from 1997-2010. Mean = 130 (red line) (Texas Colonial Waterbird Society unpubl. data).

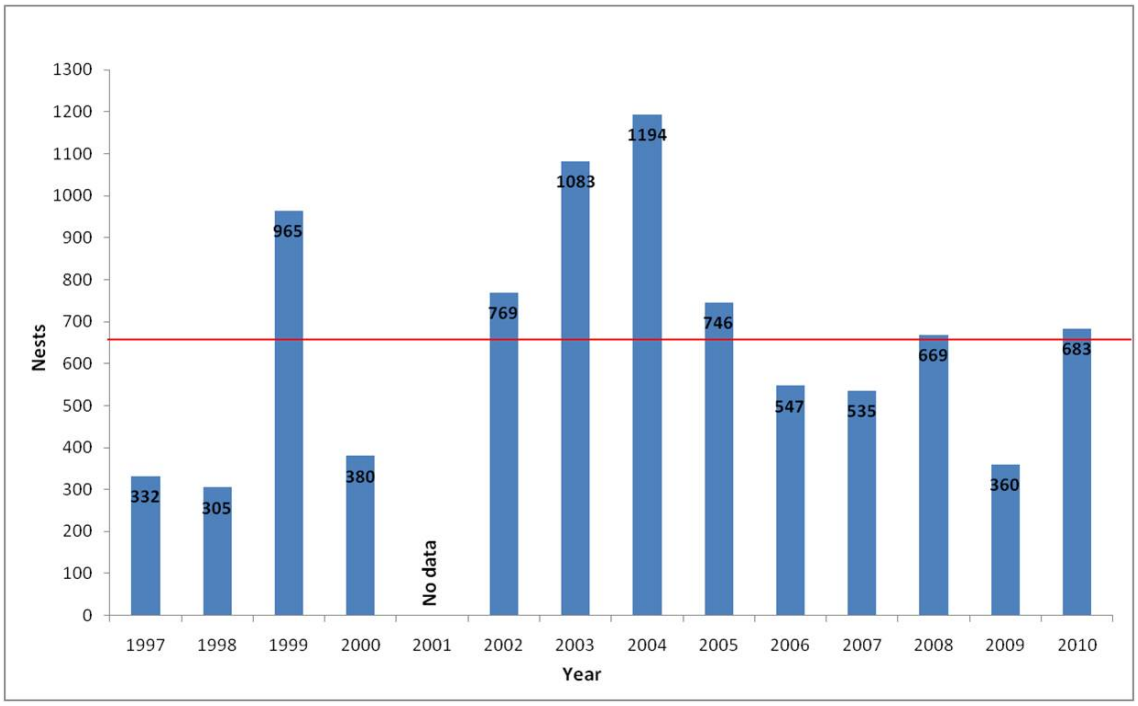

Fig. 9. Number of nests, all species, at Heron Island from 1997-2010. Mean = 659 (red line) (Texas Colonial Waterbird Society unpubl. data).

Great Egret nests (2009, n = 25; 2010, n = 22), representing 32.5% and 20.0% of the breeding populations, respectively, were monitored from clutch initiation through to a mean nestling age of 49 days (range 27-56 days) in 2009, and 56 days (range 43-69 days) in 2010. The reproductive parameters analyzed in this study are condensed in Table 3.

Table 3. Reproductive parameters for Great Egrets at High Island, Texas 2009-2010 showing test statistic and significance (*P* value).

	Pooled	**2009**	**2010**	**test statistic**	***P***
Breeding Success	77.0%	76.0%	77.3%	z = -0.102	0.919
Productivity	2.00	2.12	1.86	z = -1.075	0.282
Adjusted Productivity	2.61	2.79	2.41	z = -1.939	0.052
Brood Size	2.64	2.48	2.82	z = -1.706	0.088
Adjusted Brood Size	3.06	2.89	3.24	z = -1.826	0.068
Fledging Success 21 days	86.8%	84.8%	89.0%	z = -0.361	0.718
Fledging Success 28 days	79.9%	84.8%	74.1%	z = -2.495	0.013
Fledging Success 35 days	78.1%	82.6%	72.8%	z = -2.109	0.035
Fledging Success 42 days	76.0%	82.6%	68.4%	z = -2.211	0.027
Adjusted Fledging Success (21 days)	96.1%	98.2%	94.0%	z = -1.450	0.147
Adjusted Fledging Success (28 days)	89.6%	98.2%	79.9%	z = -3.534	< 0.001
Adjusted Fledging Success (35 days)	87.5%	95.6%	78.4%	z = -3.015	0.003
Adjusted Fledging Success (42 days)	86.6%	95.6%	76.5%	z = -3.069	0.002
Deaths per nest	0.64	0.36	0.95	z = -2.491	0.013
Deaths by Brood Size - pooled				H = 14.061	0.003
Deaths by Brood Size - 2009				H = 8.409	0.015
Deaths by Brood Size - 2010				H = 10.107	0.018

z is Mann-Whitney U, *H* is Kruskal-Wallis.

Breeding success (percentage of nests that were successful, i.e., raised at least one chick to fledging age of 42 days) for the two years pooled was 77% and did not differ significantly between years (Table 3).

Productivity (number of nestlings surviving to fledging) across years was 2.00 fledglings per nest (n = 47 nests) and was similar between years (P = 0.282); 2009 was 2.12 (n = 25 nests) and 2010 was 1.86 (n = 22 nests) (Table 4). Adjusted productivity (fledglings per successful nests only) for the two years pooled was 2.61 (± 0.107) (n = 36 nests); 2009 was 2.79 (± SE 0.123) (n = 19 nests) and 2010 was 2.41(± SE 0.173) (n = 17 nests) which were not significantly different (U-test, z = -1.939, P = 0.052).

Table 4. Frequency distribution of Great Egret productivity at High Island for 2009 and 2010.

	Number of fledglings							
	0	**1**	**2**	**3**	**4**	**Total**	**Nests**	**Mean**
2009	6	1	2	16	0	53	25	2.12
2010	5	2	6	9	0	41	22	1.86

Brood sizes ranged from 0 to 3 (2009) and 0 to 4 (2010) and the two-year pooled mean brood size was 2.64 (± SE 0.171) (n = 47 nests). Year-specific brood sizes were

2.48 (± SE 0.201) and 2.82 (± SE 0.284) (2009, n = 25 nests; 2010, n = 22 nests). Though the 2010 season had a larger mean brood size these results did not differ significantly (*U*-test, z = -1.706, *P* = 0.088). Hereafter, brood sizes will be represented by the following: BS/4 = brood size of 4, BS/3 = brood size of 3, BS/2 = brood size of 2.

Adjusted brood size (i.e., successful nests only) for the two years pooled was 3.06 (± SE 0.097) (n = 36 nests). For 2009 adjusted brood size was 2.89 (± SE 0.072) (n = 19 nests) whereas for 2010 it was 3.24 (± SE 0.182) (n = 17 nests), suggesting no between-year significance (*U*-test, z = -1.826, *P* = 0.068).

The most frequent brood size in 2009 was BS/3 (n = 18 nests, 72% of sampled nests) followed by BS/2 (n = 4, 16%). Twelve percent of study nests in 2009 failed to hatch any nestlings (n = 3). For 2010, these brood size frequencies were BS/4 and BS/3 (n = 8 each, 36.4% each, 73% combined) then BS/2 and BS/0 (n = 3 each, 13.6% each, 27% combined) (Table 5).

Table 5. Frequency distribution of Great Egret brood size at High Island for 2009 and 2010.

	Number of nestlings							
	0	**1**	**2**	**3**	**4**	**Total**	**Nests**	**Mean**
2009	3	0	4	18	0	62	25	2.48
2010	3	0	3	8	8	62	22	2.82

Fledging success (at 42 days) (hereafter fledging success periods will be reported as FS/42 for 42 days, FS/35 for 35 days, and so on) for the two years pooled was 76%. Year-specific mean FS/42 was 82.6% (2009) and 68.4% (2010)—a significant difference (*U*-test, z = -2.211, *P* = 0.027). FS/21 pooled was 86.8%; year-specific FS/21 was 84.8% (2009) and 89.0% (2010), an insignificant difference (*U*-test, z = -0.361, *P* = 0.718). FS/28 pooled fledging success was 79.9% and year specific FS/28 was 84.8% (2009) and 74.1% (2010), a significant difference (*U*-test, z = -2.495, *P* = 0.013). The FS/35 pooled fledging success was 78.1% and year specific FS/35 was 82.6% (2009) and 72.8% (2010), also significantly different (*U*-test, z = -2.109, *P* = 0.035). However, for the year 2009 breeding season, three late-starting nests were not monitored through to at least 42 days (27, 27, and 35 days respectively), but were included in calculations. It was assumed that these nestlings survived to 42 days as nestling deaths primarily occurred before 28 days for both years (Fig 10), an assumption that could alter the results presented.

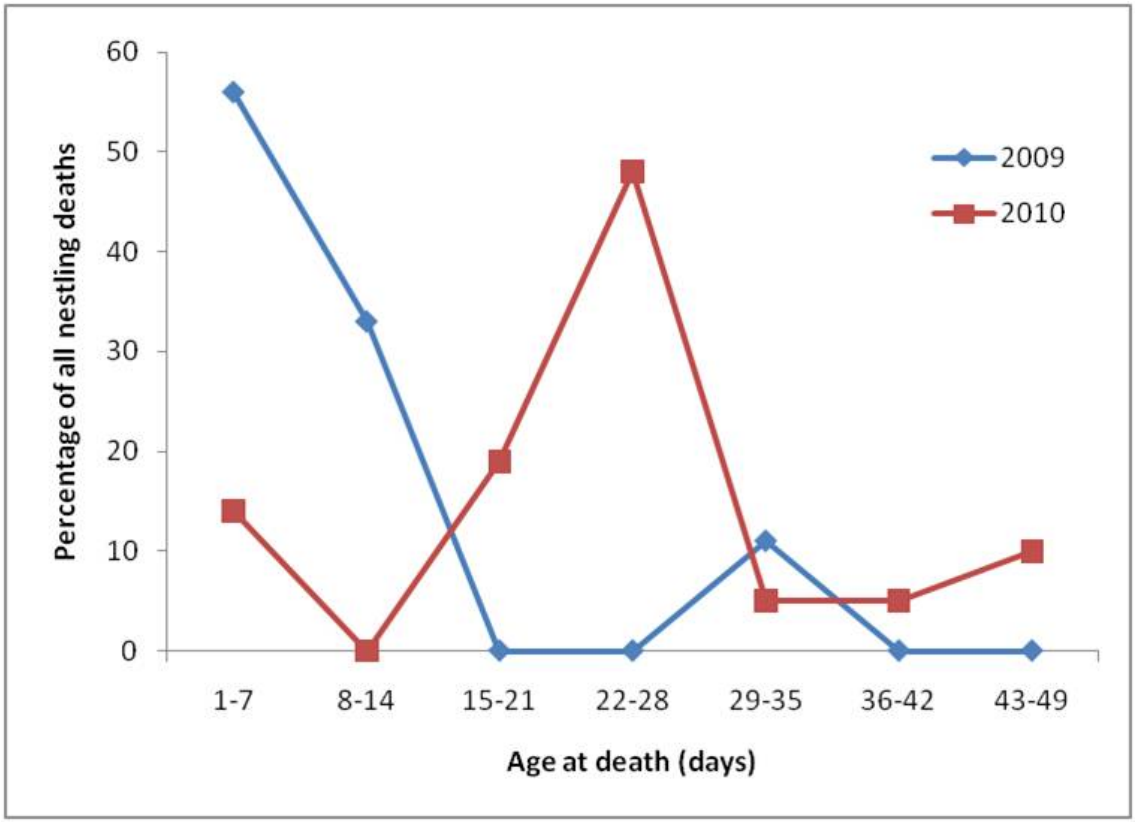

Figure 10. Percentage of Great Egret nestling deaths in relation to the age of the A-chick in each nest when nestling deaths occurred, including nest failures, at High Island, Texas. Cumulative deaths by 28 days were 89% in 2009 and 81% in 2010.

Adjusted fledging success at 42 days pooled for the two years was 86.6%. Successful nests from 2009 season fledged 95.6% of the nestlings, while in 2010 successful nests fledged 76.5% of nestlings, a significant difference (*U*-test, z = -3.069, *P* = 0.002).

Fledging success per brood size (i.e., brood-size specific FS/42) in 2009 was 92.6% (n = 18 nests) for BS/3 and 37.5% (n = 4 nests) for BS/2 (50% of BS/2 nests

failed). However, in 2010, BS/4 fledged 62.5% (n = 8 nests), BS/3 also fledged 62.5% (n = 8 nests), and BS/2 (n = 3 nests) fledged 100% of hatchlings. Neither year had BS/1. Pooled fledging success was 62.5% (n = 8 nests) for BS/4, 83.3% (n = 26 nests) for BS/3, and 64.3% (n = 7 nests) for BS/2 (Table 6).

Table 6. Fledging success (nests) by brood size for Great Egrets nesting at High Island, Texas, and those of Mock and Parker (1986) and Morrison and Shanley (1978).

	High Island		**High Island**	**Mock and Parker (1986)[a]**	**Morrison and Shanley (1978)[a]**
	2009	**2010**	**POOLED**	**POOLED**	**1997**
BS/4	n/a (0)	62.5% (8)	62.5% (8)	63.5% (13)	n/a
BS/3	92.6% (18)	62.5% (8)	83.0% (26)	80.3% (126)	63% (13)
BS/2	37.5% (4)	100% (3)	64.3% (7)	85.0% (80)	70% (17)
BS/1	n/a (0)	n/a (0)	n/a (0)	31.0% (32)	0 % (2)

[a]Values for Mock and Parker, and Morrison and Shanley were calculated from data supplied in the original publications.

Hatching spread (hatching interval between chicks) was recorded for both breeding seasons. In 2009, the mean number of days between hatching of the A-chick and the C-chick was 4.21 (± 0.49) days; in 2010, this interval was shorter at 2.73 (± 0.50) days. In 2009, A- to B-chick intervals were 0.47 (± 0.19) days, and in 2010 this interval was 1.11 days (± 0.30) days. Unlike the 2009 season, 2010 also hatched D-

chicks (n = 8 nests). The hatching interval between A-chicks and D-chicks averaged 6.00 (± 0.71) days (Table 7; Fig. 11).

Table 7. Summary of hatching chronology and number of days between hatching of Great Egret chicks at High Island, Texas, for the 2009 and 2010 breeding seasons. A-chick is first to hatch, then B-chick, and so on.

	A - B		**B - C**		**C - D**		**A - C**		**A - D**	
	2009	**2010**	**2009**	**2010**	**2009**	**2010**	**2009**	**2010**	**2009**	**2010**
Mean	0.47	1.11	3.79	1.80	n/a	3.25	4.21	2.73	n/a	6.00
± (SE)	0.19	0.30	0.50	0.55	n/a	0.65	0.49	0.50	n/a	0.71
n (nests)	17	18	14	15	n/a	8	14	15	n/a	8

Note: 5 nests from 2009, and 1 nest from 2010, were not included in this analysis as they lacked data.

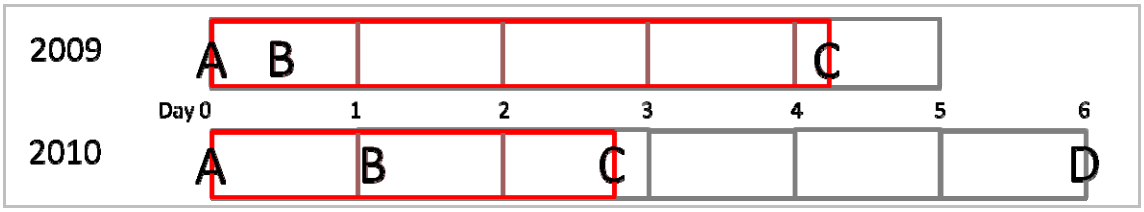

Figure 11. Hatching spread of A- to C-chicks in 2009 and 2010 showing concentrating of similarly aged chicks in 2010.

Young that died in nests that still retained siblings, and any young that disappeared sequentially (in broods greater than 1), were considered to have died of starvation (as per Pratt and Winckler 1985), be that socially enforced starvation or not. In most cases, I had direct information on the likely causes of nestling mortality: during the 2010 season I observed considerable aggression, both in severity and frequency, in multiple nests which subsequently experienced brood reductions—in two instances the desiccated and bloody, partially defeathered carcasses remained in respective nests for up to 72 hours. There was only one nest, in 2010, which I suspect was depredated. In this nest all but one of the 3 nestlings abruptly disappeared (i.e., not sequentially) at age 22 days for the A-chick and no carcasses or wandering young were observed anywhere near the nest.

Minimal sibling aggression was observed during 2009, with most occurrences ceasing during the first week. This 2009 aggression was neither severe nor frequent. However, in 2010, in addition to this early aggression, multiple nests exhibited considerable sibling aggression over a longer portion of the nestling period, primarily from the third week onward. The proportion of study nests experiencing brood reduction was 20% in 2009 (n = 5 nests) and 59% (n = 13 nests) in 2010. The number of nests experiencing partial brood reduction was 2 in 2009 and 11 in 2010—representing 8% and 50% of study nests. Brood-size specific rates of partial brood reduction for 2009 were: 6% of BS/3 (1 of 17) nests and 50% of BS/2 (1 of 2). For 2010, these brood-specific rates were 100% of BS/4 (7 of 7) nests, 57% of BS/3 (4 of 7) nests, and 0% partial brood reductions in BS/2 (0 of 3) nests.

The pooled mean number of deaths per nest was 0.64 and the year-specific mean nestling deaths per nest were 0.36 (± SE 0.162) in 2009, and 0.95 (± SE 0.232) in 2010. The percentage of nestling deaths for 2009 was 14.5% (9 of 62), while for the 2010 season 33.9% (21 of 62) of nestlings died. The two years pooled showed significant differences in deaths per nest (H = 14.061, df = 3, P = 0.003). The absence of post-hoc tests precludes determination of which pairs differed, but an examination of the records and the mean ranks show that BS/4 had the most deaths per nest, followed by BS/2 then BS/3. This same analysis procedure was conducted for the 2009 and 2010 tests. In 2009 there was a significant difference in deaths per nest based on brood size (H = 8.409, df =2, P = 0.015). The 2009 brood size of 2 experienced the most deaths per nest. The 2010 breeding season also showed significant difference in deaths per nest based on brood size (H = 10.107, df =3, P = 0.018), with brood size of 4 experiencing the most deaths per nest, followed by brood size of 3 then 2.

In 2009 the mean age at death was 12 days (median = 9 days); 56% (n = 5) of deaths occurred in the first 7 days (age of A-chick in respective nest), 33% (n = 3) between 8-14 days, 11% (n = 1) between 29-35 days, and 0% for 36-42 days and 43-49 days. In 2010 the mean age at death was 23 days (median = 26 days); 14% (n = 3) died in first 7 days, 0% between 8 – 14 days, 19% (n = 4) between 15-21 days, 48% (n = 10) between 22-28 days, 5% (n = 1) for periods 29-35 and 36-42 days, and 10% (n = 2) at age 43-49 days.

Cumulatively, 89% (8 of 9) of nestling deaths in 2009 occurred in the first 14 days post hatching with the remaining death (11%) occurring by 35 days. In 2010 the

cumulative deaths were: 14% in the first 7 days post hatching, 33% by age 21 days, 81% by the 28th day, 86% by day 35, 90% by 42 days, and 100% by the 49th day (Fig 12).

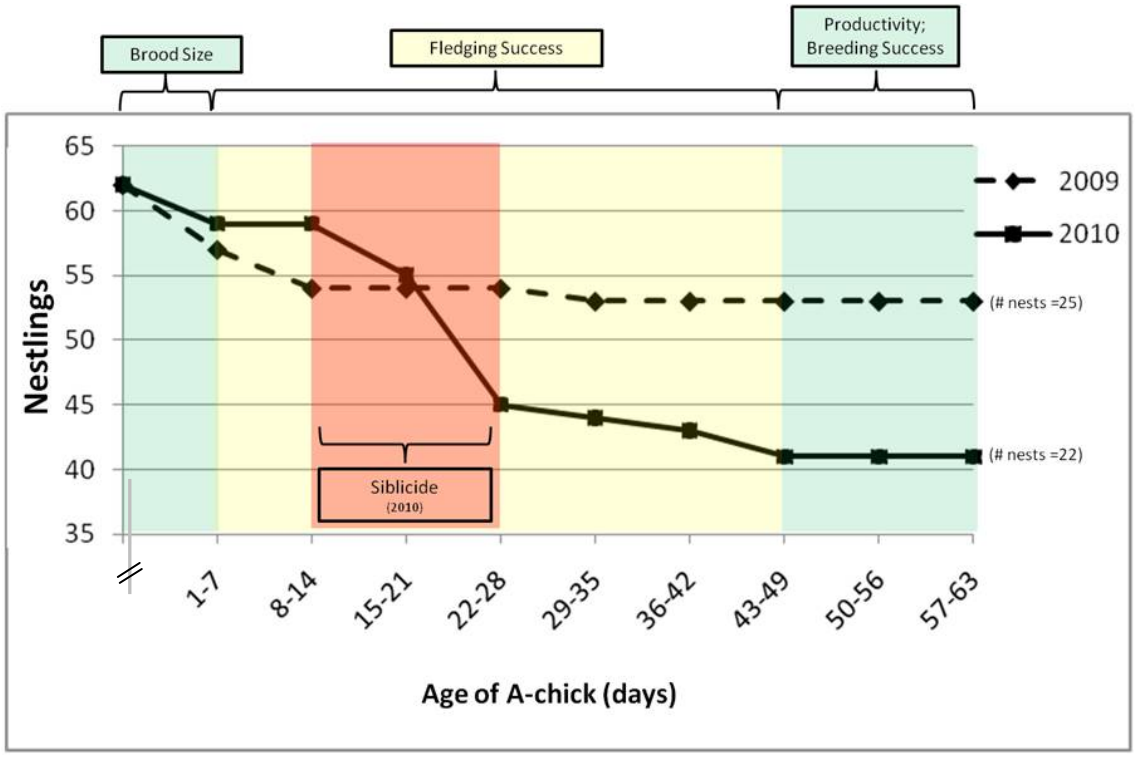

Fig. 12. Cumulative brood reduction of Great Egret nestlings, by age, in 2009 and 2010, at High Island, Texas. Both years had a nestling population of 62. Note: nestling ages are days of age post-hatching for eldest nestling (A-chick). Deaths occurring up to 14 days (both years) include nest failure. The 2010 event shown at 43-49 days was also a nest failure.

The parameters of breeding success, brood size, fledging success, adjusted fledging success, productivity, and adjusted productivity were within the range reported for this species in the literature (Appendix A).

Weather Parameters

Temperature and precipitation data were sourced from Weather Underground Inc. for station MTR474 Anahuac/High Island (29.669 °N, -94.438 °W) (Weather Underground Inc. 2010). This station is located 12 km from the study site (Fig. 7). Long-term (30-year) mean monthly values for temperatures and precipitation were not available from this station. As such, these data were obtained from The Weather Channel (weather.com 2011) for High Island.

Mean high and low temperatures for the months of March through August did not differ greatly between the two years of this study, or from the 30-year averages, nor were there any extremes. The regression line of average, high, and low temperatures for each year (Figs. 13A-13C) showed similar R^2 values (average temperature R^2 of 0.8493, 0.8141, and 0.9117; high temperature R^2 of 0.8636, 0.8754, and 0.9163; low temperature R^2 of 0.8903, 0.8195, and 0.8834, for 2009, 2010, and 30-year, respectively), suggesting either the absence of extremes, or a similarity of extremes. Further, visual examination of the graphed values shows little deviation between years and from the 30-year values, and the absence of extremes in temperature values.

Both breeding seasons received similar precipitation totals to the 30-year average of 27.32 inches (Fig. 14); total rainfall for the months of March-August was 33.4 in 2009

and 27.0 inches in 2010. As such, at no time did the water level of Claybottom Pond recede to the point that Heron Island was no-longer surrounded by water. These abiotic parameters are summarized in Appendix B.

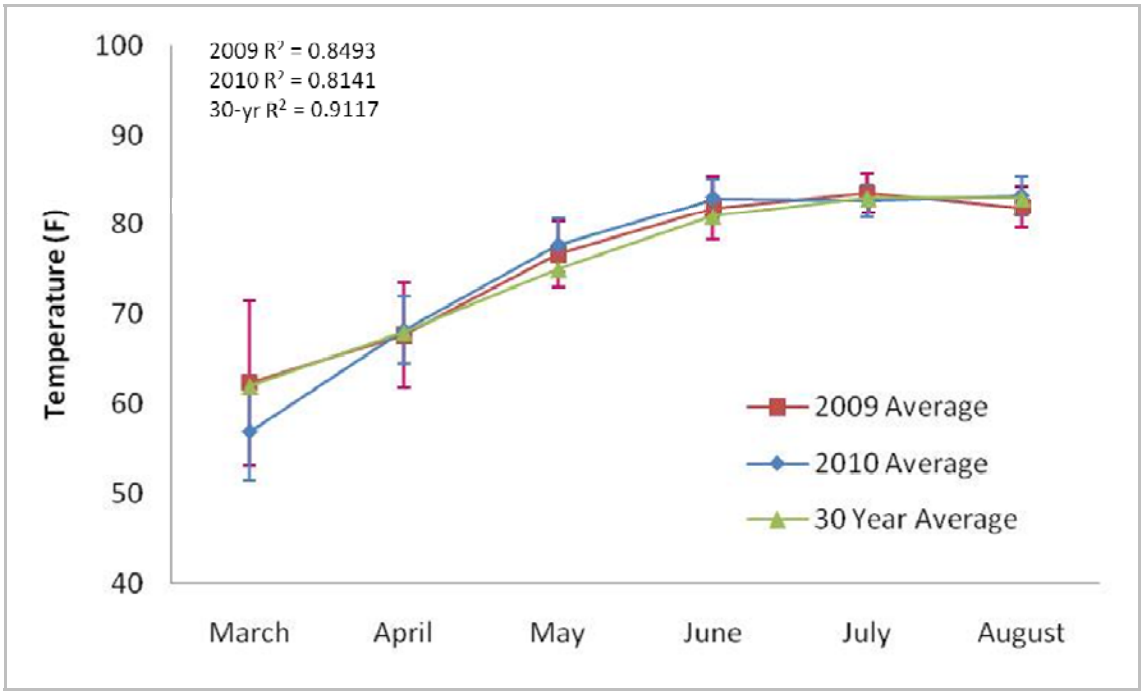

Fig. 13A. Monthly average temperatures for 2009 and 2010 for Anahuac/High Island, plus the 30-year average temperature: red squares represent 2009, blue diamonds for 2010, and green triangles represent the 30-year average. The connector-lines are for illustrative purposes only. Error bars show the standard deviations for the 2009 and 2010 values.

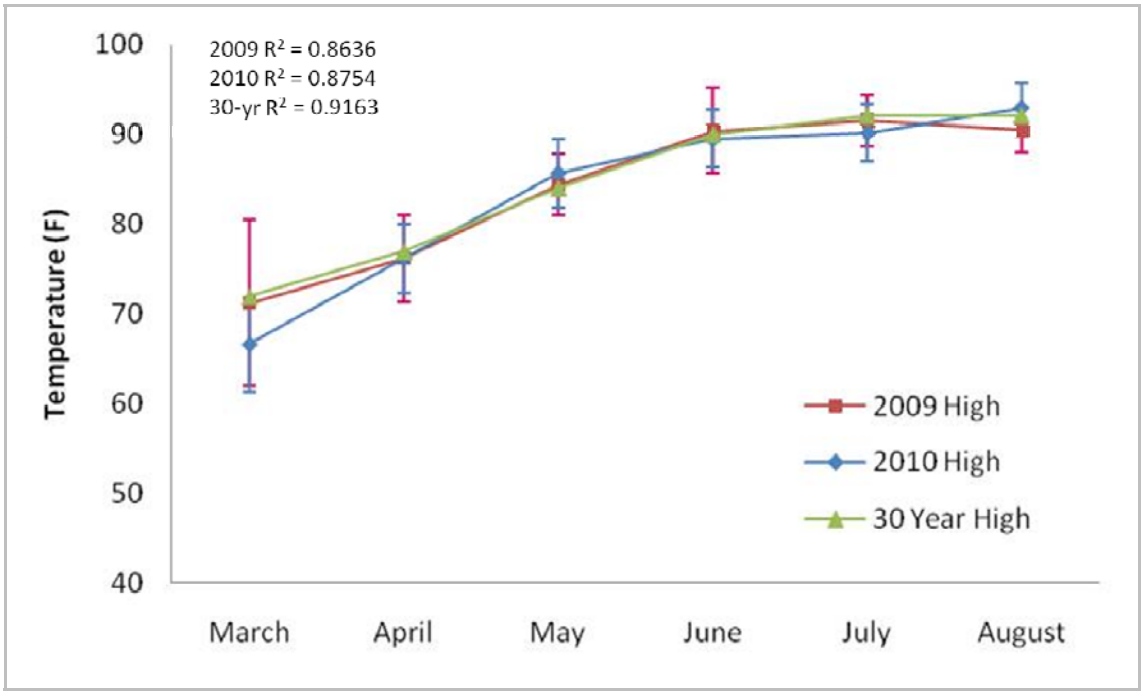

Fig. 13B. Monthly high temperatures for 2009 and 2010 for Anahuac/High Island, plus the 30-year average high temperature: red squares represent 2009, blue diamonds for 2010, and green triangles represent the 30-year average. The connector-lines are for illustrative purposes only. Error bars show the standard deviations for the 2009 and 2010 values.

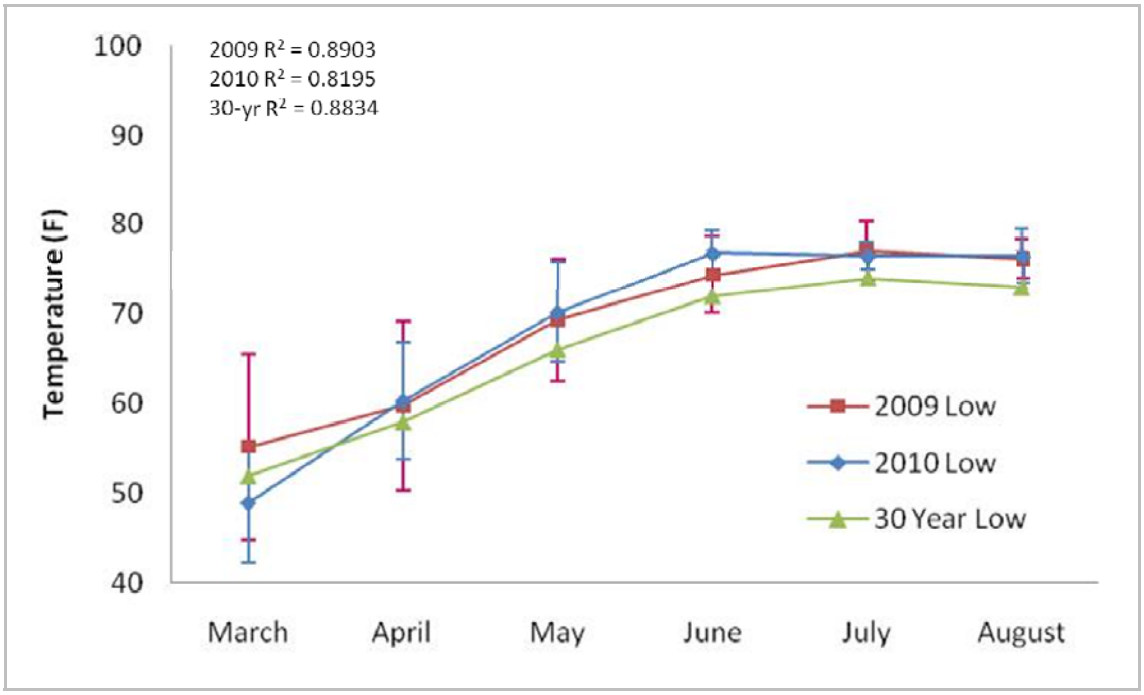

Fig. 13C. Monthly low temperatures for 2009 and 2010 for Anahuac/High Island, plus the 30-year average low temperature: red squares represent 2009, blue diamonds for 2010, and green triangles represent the 30-year average. The connector-lines are for illustrative purposes only. Error bars show the standard deviations for the 2009 and 2010 values.

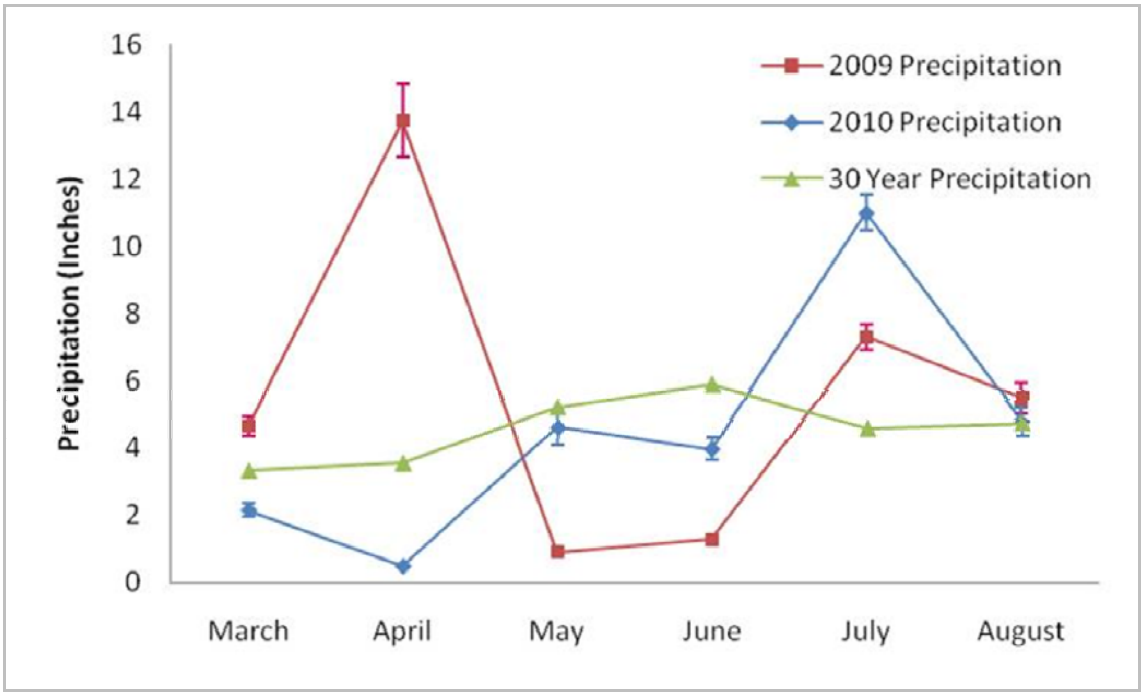

Fig. 14. Monthly precipitation for 2009 and 2010 for Anahuac/High Island, plus the 30-year average precipitation: red squares represent 2009, blue diamonds for 2010, and green triangles represent the 30-year average. The connector-lines are for illustrative purposes only. Error bars show the standard deviations for the 2009 and 2010 values.

Prey Availability

Analysis of fish abundance data suggest that, for the months of May – July, the 2009 breeding season had lower fish density than did 2010 (3 month average abundance per hectare are 894 and 97,907 for 2009 and 2010, respectively). The seven year (1999-2005) average fish abundance for these same months was 39,632 fish per hectare (TPWD unpubl. data).

DISCUSSION AND CONCLUSIONS

Reproductive Performance

This study tested the hypothesis that, due to massive environmental perturbations caused by Hurricane Ike in the summer of 2008, the reproductive performance of 2009 would be depressed in relation to the successive year. Testing was achieved through quantification of breeding success, brood size, productivity, and fledging success. I found that breeding success, brood size, and productivity did not differ between years, but fledging success did.

Counter to the hypothesis that landscape habitat conditions would be less conducive to reproductive performance in 2009 (following Hurricane Ike), it was the 2010 breeding season that experienced greater nestling death rates and reduced fledging success. Proximate factors typically cited as affecting the reproductive performance of GREGs include: water levels, extreme weather fluctuations, predation, age of parent, and prey availability (Burger 1982; McCrimmon et al. 2001; Frederick 2002).

In studies where water levels are cited as a causative factor (Custer and Osborne 1978; Powell 1987; Bancroft et al. 1994, 2002; Herring et al. 2010), the study area was dominated by "managed" flows which act to concentrate/disperse prey; this hydrologic regime is not present in the estuarine environment proximal to my study area. Alternatively, GREG rookeries located inland have reportedly either been abandoned or breeding populations greatly reduced when aquatic levels dropped precipitously (Dusi and Dusi 1968; Smith 1995; Smith et al. 1995; Naugle et al. 1996; Grüll and Ranner

1998). The water levels surrounding Heron Island did not experience any such drops during the course of this study.

In reports where weather negatively affected reproductive performance, the weather events are “unusual” or “extreme” perturbations such as a late freeze (Simmons 1959; Parsons 1985), severe wind events (Jenni 1969; Burger 1982), and unusually high rainfall (Jenni 1969; Burger 1982; Frederick and Callopy 1989a). Heat stress, however, is not considered a problem unless human disturbance keeps the parents from shading eggs or young chicks (Burger 1982). As Figures 13A-C and 14 illustrate, these weather events either did not occur, or did not differ in frequency or magnitude between study years. Likewise, human disturbance, as discussed by Goering and Cherry (1971), Burger (1982), Mueller and Glass (1988), Erwin (1989), Frederick and Collopy (1989c), Carney and Sydeman (1999), and Heath and Parkes (2002), was not a factor at this rookery.

Predation is an obvious factor negatively impacting reproductive performance (Dusi and Dusi 1968; Clark and Wilson 1981; Burger 1982; Pratt and Winkler 1985; Frederick and Collopy 1989b). However, due to the limited access of terrestrial predators to the rookery island, nestling losses due to predation appeared, at worst, to be minimal. Inferred predation, presumably avian in nature, was present in only one nest over the two years. This depredated nest was particularly exposed relative to conspecific nests and more so than the percent vegetative openness documented by McCrimmon (1978). Frederick and Collopy (1989b) similarly reported little evidence of avian predation on wading bird nests in the Florida Everglades.

Intrinsic variables such as age and experience are also considered to affect reproductive performance of GREGs; generally, older birds have increased reproductive success relative to young birds (Burger 1982; Parsons 1985). However, the non-invasive design of my study precluded assessment of parental age or hormone levels. It is possible, therefore, that differences in these intrinsic variables may have contributed to the observed between-year variability.

Prey availability is commonly considered a primary driver of reproductive performance (Lack 1947; Skutch 1949; Newman 1980; Frederick and Collopy 1989a; Bancroft et al. 1994; McCrimmon et al. 2001; Custer and Galli 2002). While TPWD fisheries data used in this analysis showed considerable between-year differences in abundances, the pattern was inversely related to fledging success. Many breeding birds forage for long periods to collect food for young, yet foraging duration doesn't necessarily indicate foraging success nor sufficient quantity for self-maintenance and the requirements of nestlings (Newton 1980). Additionally, food availability is especially critical in later stages of nestling development (Fleury 1996), the period coinciding with greater prey densities in TPWD bag seine data. Thus, prey abundance does not appear to explain the variability in death rates and fledging success of this study.

Due to the saltwater inundation impacts of Hurricane Ike, foraging in what were traditionally freshwater habitats was likely limited, especially during the 2009 breeding season, as assemblages and abundances of aquatic invertebrates were probably greatly altered (Fig. 5B) (see also Fitzsimmons 2010). Teal (1965) studied gut contents of GREG nestlings in Georgia and reported that they consisted "mainly of small fish of

species found in salt marshes and estuaries." Among the species he identified were *Fundulus* spp. (a killifish) and "small menhaden." Similarly, at Lavaca Bay, Texas, Mock (1985) reported that the primary prey species identified in GREG food boluses were Gulf menhaden and a silverside species. Post (1990) reported that the diet of GREG nestlings in South Carolina was comprised primarily (73%) of saltwater fish species, 25% saltwater crustaceans, and 2% mollusks and annelids. As such, it appears that GREGs on the upper Texas coast could satisfy food intake requirements in primarily estuarine habitats, theoretically minimizing the impacts of Hurricane Ike on the diet of these reproducing GREGs. Smith (1997) calculated the diet diversity of adult GREGs and found it to be larger than that of several other egret and heron species also examined, likely because GREGs readily switch prey types as conditions and habitat conditions change.

Minello and Rozas (2002) report that although many fishes and decapod crustaceans are common inhabitants of salt marshes in the northwestern Gulf of Mexico, spatial distributions are uneven and populations are difficult to estimate. As such, nekton densities are seldom evenly distributed though a general pattern of high nekton densities near the marsh edge has been identified (Minello and Rozas 2002) and nekton densities of Gulf coast marshes are considerable (Rozas 1993).

Several of the prey guild selected for analysis in my study were also included in Minello and Rozas' (2002) study relating abundance with distance from marsh edge in Galveston's West Bay. Interestingly, abundance relative to distance from marsh edge exhibited an inverse relationship for sheepshead minnow and Gulf killifish, out to 3 m

seaward. That is, for some fish species at least, abundance may increase with distance from marsh edge (up to a point) whilst for other species abundance may decrease (table 1 in Minello and Rozas 2002). Rozas and Zimmerman (2000) reported that for upper Galveston Bay and East Bay, several of the selected prey species for this analysis (Gulf menhaden, spot, bay anchovy, and Atlantic croaker) had higher densities over the nonvegetated bottoms than at the marsh itself.

If prey is a limiting causative factor, the impact would be negative on reproductive performance; however, the year with reduced prey densities corresponded to the year of greatest reproductive performance. Considering the higher prey abundances in 2010, the foraging habitat flexibility of GREGs, and the apparent spread of prey species between marsh and near-marsh "open water", it appears that prey distribution and availability to GREGs may not have been limited. But, it is possible that the estuarine species selected and quantified as food resources for this study may not appropriately represent food resources for breeding GREGs at this colony. Alternatively, the TPWD bag seine data may not accurately represent food availability or the quality of foraging habitats for these reproducing GREGs.

Brood-size Dependent Mortality

I was able to identify brood-size dependent mortality (i.e., deaths by brood size) as the primary causative factor in the between-year difference in fledging success. Though brood size numbers varied between years, the between-year mean brood size did not differ significantly, nor did the adjusted brood size. Importantly, however, is that

2010 had numerous broods of 4 (n = 8 nests; 36% of sampled nests), whereas 2009 had zero BS/4 nests. Additionally, brood reduction rates per-nest differed considerably between years, as did the proportion of nests experiencing partial brood reduction and the brood sizes in which partial brood reduction occurred. These disparities indicate that brood size contributed to elevated rates of sibling aggression, resulting in brood-size dependent mortality and elevated rates of deaths-per-nest. This brood-size dependent mortality appears to be strongly associated with total hatching-spread (asynchrony). Increased brood size results in increased total hatching spread; however, while total hatching spread is greater as brood size increases, A- to C-chick spread is reduced when brood size exceeds BS/3 (approximately 1.5 days shorter in 2010) (Table 7). In years of larger broods (greater total hatching spread, reduced A- to C-chick spread) there is a concentrating of similarly aged/sized chicks (Fig 11). This is especially important during the period when the feeding method transitions from indirect to direct (a time of rapidly increasing nestling energy demands) as it appears to trigger competition from similarly developed siblings. Therefore, it appears that nestling aggression increases as a response to increased direct food competition.

Nestling mortality of facultatively siblicidal GREGs appears to be bimodal, though the second mode is not always expressed: the first mode occurs in the first two weeks (accidents, trampling, complete nest failure) and the second mode occurs from week three through week six (i.e., 15-42 days) (Fig. 12) as a function of brood-size dependent siblicide. Nesting mortality in 2009 was only expressed unimodally, whereas both modes were expressed in 2010 (Figure 10). That is, for those nests experiencing

brood reduction in 2009, only one period of brood reduction occurred; the second mode, indicative of siblicide/starvation, was absent in 2009—likely due to the increased hatching spread for A- to C-chicks, relative to 2010.

Because GREG siblicide occurs after most other early forms of death have occurred (Godfray 1986), the 2009 deaths are indicative of "normal" early-stage deaths such as parent trampling, falling out of the nest, or total nest failure. The 2010 nestling deaths also exhibited the "first mode" of nestling deaths, but also a second mode, suggesting different forces at work between years. These "second mode" deaths occur during the siblicide stage of development (Fig. 12). Unlike the 2009 season, three nests in 2010 experienced at least two separate brood reductions (non-concurrent), a situation that is not unusual in GREGs (Mock 1985). Predation at this rookery, during the 2009 and 2010 breeding seasons, appears minimal, limited to one occurrence during 2010.

Morrison and Shanley (1978) reported 72% of nestling mortality during the first 10 days post-hatching and none after 20 days. Likewise, Maxwell and Kale (1977) reported that 14% of GREG nestlings had died by the 10^{th} day after the last chick hatched (i.e., approximately within two weeks of A-chick hatching). However, in a 13 year study, Pratt and Winkler (1985) reported an essentially normally distributed curve of nestling mortality whereby 70% of the 471 nestlings died in weeks 2-4, with the greatest nestling mortality occurring in the third week (15-21 days post-hatching) which coincides with the switch to direct feeding. Similarly, Mock and Parker (1986) reported that the greatest nestling mortality occurred in the first 2 weeks and most brood reduction occurred during the first 4 weeks. The deaths occurring after two weeks appear

to be associated with the switch from indirect to direct feeding behavior, whereby older siblings gain greater than average food shares and, subsequently, the younger siblings have higher risks of starvation, as reported by Mock (1985).

Baxter (1994) reported no difference between fledging success at 7 or 11 days versus 6-8 weeks in his study in New South Wales, Australia. However, if chick mortality rates are not constant throughout the nestling period, that is, strongly concentrated in the latter stage of the nestling phase as it was in the 2010 season at High Island, then the use of an early fledging age criterion is likely invalid and may provide results that differ substantially from the actual fledging success (O'Connor 1978; Erwin and Custer 1982).

Wiese (1975) found significant differences in the nestling-age at which parents left the nest unguarded, relative to brood size: BS/4 at 21.4 days, BS/3 at 24.4 days. He surmised that at this development stage the nestling's food requirements are rapidly increasing, and each nestling in BS/4 in theory receives less food than those in BS/3 due to the fixed physiological capacity of the parent's crop. As such it is possible that there may be an increase in food-begging in BS/4 relative to BS/3 nestlings, thereby triggering a behavioral shift in the parents, perhaps to increase food-delivery rates. Assuming reduced food availability per nestling with increased brood size and the expected increase in food begging does occur, it follows then that sibling aggression in this facultatively siblicidal species would increase with increased brood size.

The pooled fledging success by brood size results for BS/4 and BS/3 fit very closely with Mock and Parker's (1986) reported values (Table 6). The 2010 High Island

pooled results, and Mock and Parker's pooled results, strongly indicate that nestling deaths increase when brood size exceeds BS/3. The disparity in my pooled fledging success for BS/2 is likely explained in that 2 of the 7 nests with BS/2 failed; if these two are removed from this analysis the resultant pooled BS/2 is 90%, a value similar to Mock and Parker's.

Although adjusted fledging success for all periods of fledging showed the same trends in significance as "non-adjusted" fledging success, there were notable differences in the actual rates and the periods when rates change. These adjusted fledging success results showed constancy in the rates of survival and a very high overall survival in the 2009 nestlings that was not shown in 2010. The 2009 adjusted fledging success averages some 10% higher than the non-adjusted data, indicating nest failures contributed greatly to reducing the overall survival in 2009. Conversely, adjusted fledging success in 2010 did not show constancy in value and were only slightly higher than the corresponding "non-adjusted" values, indicating that nest failure was not a large contributor to nestling deaths in 2010, thus partial brood reduction played an increased role in the 2010 fledging success. Though "adjusted" parameters produce inflated performance values (by virtue of removing unsuccessful nests from analysis), they do enable determination of what drove the variability, particularly regarding fledging success. These data further support the underlying bimodal occurrence of nestling mortality presented above, and suggest that brood size is a significant driver of brood reduction.

Weise (1975) reported that sibling competition for food was "strong" for BS/2 and higher, and that a "pecking order" was established by the second week. Custer and

Peterson (1991) report that weight gain and growth of GREG nestlings at a Texas coastal island rookery was slower in C-chicks than for A- and B-chicks through 18 days post-hatching of A-chick, when measurements ceased.

I observed disproportionate sibling fighting rates in 2010 compared to 2009, primarily from the third week onwards. The significant within- and between-year difference in both the number of deaths per nest, and the number of deaths by brood size, support escalated aggression as brood size increases above BS/3—a finding similar to Mock (1985) whereby 60% of all BS/3 and BS/4 nests experienced brood reduction. My observations of sibling aggression from both years indicated that early stage aggression was primarily bill-to-bill stabbing, similar to a joust.

In 2010, this sibling aggression then escalated to head blows causing bleeding and de-feathering of the recipient's head. This aggression commonly resulted in an apparent appeasement or avoidance behaviors in the submissive sibling; these behaviors included head and neck withdrawal, a loud, high-pitched screeching call, and cowering (see also Wiese 1975). The cowering I observed took the form of retreating to the edge of the nest, often extending the head and neck low and beyond the nest rim, a behavior and posture that typically resulted in cessation of aggression. On other occasions, the submissive sibling would flee the nest entirely, amid much wing flapping and screeching. However, upon the parent's departure from the nest, the submissive sibling was, in most cases, allowed to return to the nest center, with no aggression demonstrated until a parent returned to the nest. In numerous instances upon the return of a parent, the

submissive sibling would promptly commence appeasement behavior, primarily fleeing, prior to any overt aggression.

Conclusions

This study found that Hurricane Ike did not negatively impact the breeding performance of GREGs at High Island in the 2009 breeding season; the between-year differences in this study were not determined by environmental parameters. The primary difference between years was more nestling deaths in the latter nestling stages of the 2010 breeding season. This periodicity of deaths demonstrates a bimodal pattern in brood reduction; the first mode likely occurs in any population of GREGs due to accidents, trampling, and nest failure, while the second mode is behaviorally driven as a function of brood size and hatching spread. This study suggests for GREGs, and perhaps other asynchronously hatched facultatively siblicidal colonial wading bird species, that reproductive performance studies should continue through at least fledging (42 days post-hatching for GREGs) to better document the true reproductive dynamic, as analysis for any shorter period could erroneously show no differences in the reproductive performance and indicate, incorrectly, a static, stable reproductive performance.

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APPENDIX A

A1. Breeding success values of Great Egrets for this study and that in the literature.

BREEDING SUCCESS	YEAR	LOCATION	SOURCE
76%	2009	Texas	McInnes - this study
77%	2010	Texas	McInnes - this study
52%	1967	California	Pratt 1972
41%	1968	California	Pratt 1972
33%	1969	California	Pratt 1972
28%	1970	California	Pratt 1972
78%	1991-2005	California	Kelly et al. 2008
40%	2002	Connecticut	Heath and Parkes 2002
85%	1973	Florida	Maxwell and Kale 1977
39%	1958	Georgia	Teal 1965
47%	1977	Texas	Morrison and Shanley 1978

A2. Productivity values of Great Egrets for this study and that in the literature.

PRODUCTIVITY	YEAR	LOCATION	SOURCE
2.12	2009	Texas	McInnes - this study
1.86	2010	Texas	McInnes - this study
1.40	1967	California	Pratt 1972
1.10	1968	California	Pratt 1972
1.00	1969	California	Pratt 1972
1.00	1970	California	Pratt 1972
1.10	1971	California	Pratt 1974
1.50	1972	California	Pratt 1974
1.20	1973	California	Pratt 1974
1.35	1974	California	Pratt and Winkler 1985
0.03	1975	California	Pratt and Winkler 1985
0.84	1976	California	Pratt and Winkler 1985
0.61	1977	California	Pratt and Winkler 1985
1.63	1978	California	Pratt and Winkler 1985
2.04	1979	California	Pratt and Winkler 1985
1.00	2002	Connecticut	Heath and Parkes 2002
2.50	2006	Florida	Simon et al. 2006
1.42	1958	Georgia	Teal 1965
2.25	1983	Kansas	Gress and Schaefer 1984
2.50	1984	Kansas	Gress and Schaefer 1984 (in Dwyer 1988)
2.50	1985	Kansas	Dwyer 1988
2.48	1986	Kansas	Dwyer 1988
0.81	1977	Texas	Morrison and Shanley 1978
2.04	1986	NSW, Australia	Baxter 1994

A3. Adjusted productivity values of Great Egrets for this study and that in the literature.

ADJUSTED PRODUCTIVITY	YEAR	LOCATION	SOURCE
2.79	2009	Texas	McInnes - this study
2.41	2010	Texas	McInnes - this study
2.10	1967	California	Pratt 1972
1.75	1968	California	Pratt 1972
2.30	1969	California	Pratt 1972
1.90	1970	California	Pratt 1972
1.90	1971	California	Pratt 1974
2.00	1972	California	Pratt 1974
1.90	1973	California	Pratt 1974
2.33	1974	California	Pratt and Winkler 1985
2.00	1975	California	Pratt and Winkler 1985
2.08	1976	California	Pratt and Winkler 1985
1.50	1977	California	Pratt and Winkler 1985
2.09	1978	California	Pratt and Winkler 1985
2.47	1979	California	Pratt and Winkler 1985
1.99	1991	California	Kelly et al. 1993
1.87	1986	Florida	Frederick and Collopy 1989
1.89	1987	Florida	Frederick and Collopy 1989

A4. Brood size values of Great Egrets for this study and that in the literature.

BROOD SIZE	YEAR	LOCATION	SOURCE
2.48	2009	Texas	McInnes - this study
2.82	2010	Texas	McInnes - this study
2.40	2002	Connecticut	Heath and Parkes 2002
2.60	1973	Florida	Maxwell and Kale 1977
2.96	1975	New Jersey	Gladstone 1979
1.25	1977	Texas	Morrison and Shanley 1978
2.40	1979-1982	Texas	Mock 1985
2.52	1975	Mexico	Gladstone 1979

A5. Fledging success values of Great Egrets for this study and that in the literature.

FLEDGING SUCCESS	YEAR	LOCATION	SOURCE
83%	2009	Texas	McInnes - this study
68%	2010	Texas	McInnes - this study
81%	1967	California	Pratt 1972
57%	1968	California	Pratt 1972
76%	1969	California	Pratt 1972
66%	1970	California	Pratt 1972
58%	1967-1979	California	Pratt and Winkler 1985
57%	2000	Connecticut	Heath and Parkes 2002
70%	2001	Connecticut	Heath and Parkes 2002
40%	2002	Connecticut	Heath and Parkes 2002
86%	1973	Florida	Maxwell and Kale 1977
85%	1958	Georgia	Teal 1965
83%	1985	Kansas	Dwyer 1988
84%	1986	Kansas	Dwyer 1988
50%	1974	Louisiana	Wiese 1975
65%	1977	Texas	Morrison and Shanley 1978
73%	1977	Texas	Chaney et al. 1978

APPENDIX B

B-1. 30-year average monthly temperatures and those of 2009 and 2010.

	Average Temperature (° F)		
	30 Year	**2009**	**2010**
March	62	62.40	56.90
		(9.167)	(5.461)
April	68	67.70	68.20
		(5.861)	(3.764)
May	75	76.71	77.68
		(3.681)	(2.971)
June	81	81.87	82.97
		(3.550)	(2.173)
July	83	83.52	82.65
		(2.174)	(1.799)
August	83	81.94	83.23
		(2.235)	(2.109)

B-2. 30-year monthly high temperature average and those of 2009 and 2010.

	High Temperature (° F)		
	30 Year	**2009**	**2010**
March	72	71.2	66.6
		(9.297)	(5.258)
April	77	76.2	76.2
		(4.859)	(3.815)
May	84	84.4	85.7
		(3.433)	(3.821)
June	90	90.4	89.5
		(4.739)	(3.138)
July	92	91.5	90.2
		(2.839)	(3.135)
August	92	90.5	92.9
		(2.447)	(2.778)

B-3. 30-year monthly low temperature average and those of 2009 and 2010.

	Low Temperature (° F)		
	30 Year	**2009**	**2010**
March	52	55.2	48.9
		(10.326)	(6.672)
April	58	59.8	60.3
		(9.446)	(6.492)
May	66	69.3	70.2
		(6.857)	(5.608)
June	72	74.4	76.8
		(4.279)	(2.538)
July	74	77.1	76.5
		(3.197)	(1.480)
August	73	76.2	76.5
		(2.140)	(3.010)

B-4. 30-year monthly precipitation and those of 2009 and 2010.

	Precipitation (inches)		
	30 Year	**2009**	**2010**
March	3.33	4.65	2.16
		(0.291)	(0.206)
April	3.56	13.74	0.48
		(1.098)	(0.035)
May	5.22	0.91	4.62
		(0.098)	(0.506)
June	5.88	1.29	3.98
		(0.104)	(0.332)
July	4.59	7.29	10.99
		(0.367)	(0.531)
August	4.74	5.49	4.8
		(0.431)	(4.800)

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